

# CHAPTER 18-1

## LARGE MAMMALS: RUMINANTS - CERVIDAE

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### TABLE OF CONTENTS

Ruminantia – Ruminants.....	18-1-2
Impact of Ruminants on Bryophytes.....	18-1-4
Grazing .....	18-1-4
Trampling.....	18-1-12
Manuring.....	18-1-14
Life on Manure – Splachnaceae.....	18-1-15
Cervidae – Deer, Elk, Moose, and Caribou.....	18-1-17
White-tailed Deer – <i>Odocoileus virginianus</i> .....	18-1-17
Black-tailed Deer – <i>Odocoileus hemionus</i> .....	18-1-18
Reindeer/Caribou – <i>Rangifer tarandus</i> .....	18-1-18
Importance of Mosses in Diet .....	18-1-18
Digestibility.....	18-1-20
Effects on Soil Temperature.....	18-1-22
Microbial Responses to Grazing .....	18-1-23
Temporal Differences.....	18-1-23
Site Differences.....	18-1-24
Grazing Effects on Bryophytes and Vegetation .....	18-1-25
Roe Deer – <i>Capreolus capreolus</i> .....	18-1-27
Hog Deer – <i>Axis porcinus</i> .....	18-1-28
Summary.....	18-1-28
Acknowledgments .....	18-1-29
Literature Cited.....	18-1-29

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Figure 1. *Rangifer tarandus groenlandicus* scraping and browsing in the Arctic. Photo by Erwin and Peggy Bauer, U.S. Fish and Wildlife, through public domain.

### Ruminantia - Ruminants

Tiny bryophytes seem unlikely foodstuffs for large ruminants, but there are in fact records of their consumption by a variety of these cud-chewing beasts (Figure 2). What seems unlikely is that bryophytes ever provide a major portion of the diet of these animals, and their consumption may often be accidental.

If you have read about "reindeer moss," notably eaten by reindeer and caribou, you have been fooled by an inappropriate common name. The moss in this case is not a moss at all, but a lichen. And a lichen is not even a plant. Rather, it is a fungus with a partner. That partner can be one of the algae (usually Chlorophyta) or one of the Cyanobacteria. Together, they make a whole new type of organism that often can live in places where neither partner can live alone. The fungi provide protection from UV light and from desiccation. The photosynthetic algae or Cyanobacteria provide the carbohydrate energy source through photosynthesis.



Figure 2. Domestic cow (*Bos taurus*) chewing cud. Photo by foxypar4, through Creative Commons.



Wild ungulates may deliberately eat mosses or ingest them accidentally along with a preferred browse. Even large animals such as the Mylakhchinsk bison (Figure 3) have been found with mosses in the alimentary tract (Ukrantseva *et al.* 1978). Peary caribou (*Rangifer tarandus pearyi*; Figure 6) in the Canadian Arctic archipelago can have up to 58% mosses in their rumen (Thomas & Edmonds 1983), hardly indicative of accidental ingestion. Nevertheless, the nutritive value of bryophytes for warm-blooded animals has been questioned (Sugawa 1960).



Figure 3. European bison (*Bison bonasus*); mosses have been found in the alimentary tract of Mylakhchinsk bison. Photo by Michael Gäbler, through Creative Commons.



Figure 4. *Hypnum cupressiforme*; *Hypnum* was found in the alimentary tract of a Mylakhchinsk bison. Photo by Michael Lüth, with permission.



Figure 5. *Polytrichum commune*; *Polytrichum* sp. was found in the alimentary tract of Mylakhchinsk bison. Photo by Rob Routledge, through Creative Commons.



Figure 6. Peary caribou (*Rangifer tarandus pearyi*) in winter. Photo by L. David Mech, through Creative Commons.

High concentrations of polyphenolic lignin-like compounds in cell walls of bryophytes make the cellular contents less accessible to digestive enzymes (Prins 1982). They furthermore often have polyphenols that have antibiotic properties, thus inhibiting the ability of digestive bacteria in ruminants to break down the bryophytes.

Prins (1982) observed that in cold environments mosses are eaten by a variety of herbivores, both mammals and birds, including the ruminants Peary caribou (*Rangifer tarandus pearyi*; Figure 6), Spitsbergen reindeer (*Rangifer tarandus platyrhynchus*; Figure 7), Soay sheep (*Ovis orientalis*; Figure 8-Figure 9), and musk-oxen (*Ovibos moschatus*; Figure 10). Although mosses have similar caloric values to those of tracheophytes, they are difficult for these ruminants to digest (Hegnauer 1962).



Figure 7. *Rangifer tarandus platyrhynchus* grazing among grasses and mosses. Photo by Billy Lindblom, through Creative Commons.



Figure 8. Herd of European mouflon Sheep (*Ovis orientalis musimon*) feeding and lying down, both of which can have an effect on the vegetation. Photo by Frank Vincentz, through Creative Commons.





Figure 9. European mouflon sheep (*Ovis orientalis musimon*), a moss eater. Photo by Frank Vincentz, through Creative Commons.



Figure 10. Musk-ox (*Ovibos moschatus*), a herbivore that eats mosses. Photo through Creative Commons.

One explanation that has been suggested for ruminant herbivory on mosses is that mosses contain high concentrations of highly polyunsaturated fatty acids such as arachidonic acid (Gellerman *et al.* 1972). This fatty acid is also a component of animal cell membranes and other multi-unsaturated C-20 and C-22 fatty acids (Gurr & James 1971; Huneck 1983; Hegnauer 1986). Arachidonic acids have 4 double bonds, whereas the others have 5 double bonds. These are unique in mosses, being absent in seed plants where the highest level of unsaturation is usually two or three double bonds (Swanson *et al.* 1976). Mosses, on the other hand, may have up to 35% of their fatty acids as arachidonic acid, the highest known in any plants (Gellerman *et al.* 1972; Suire & Asakawa 1979). Gellerman *et al.* (1972) and Swanson *et al.* (1976) suggest that in mosses this acid contributes to the special properties of the chloroplast and other tissues that enable them to survive extreme environmental conditions.

Prins (1982) suggested that consumption of mosses with their arachidonic acids permits Arctic animals to have

a higher activity level at low temperatures by making their cell membranes, especially in foot pads, more fluid at low temperatures. These fatty acids decrease the temperature at which the membrane undergoes a phase change from a liquid crystalline state to a solid or gel-like state. This behavior of membranes has been demonstrated for cold-acclimated fish; these fish show a higher degree of unsaturation in the lipids of the cell membrane than do warm-acclimated fish (Caldwell & Vernberg 1970; Cossins *et al.* 1977; Smit 1980). Nevertheless, no direct evidence is available to demonstrate the real fate of arachidonic acid derived from a diet including mosses (Prins 1982). If the Arctic animals do eat mosses to gain arachidonic acid, they may have to eat large quantities because of the limited digestibility of the moss.

Some seeds have been protected from mammal predation by neighboring bryophytes (Ukrainitseva 1979). In the late Pleistocene, bryophytes reduced post-dispersal predation, whereas  $^{14}\text{C}$  dating indicated that some animals had consumed bryophytes.

Van der Wal and Brooker (2004) found that few studies on the impacts of herbivores on the vegetation addressed impacts in the Arctic. They specifically sought understanding of the impact of the moss layer. This layer maintains warmer soils that potentially benefit the tracheophytes. Their results suggest that grazers impact the moss depth, subsequently altering soil temperature, and that this temperature change may impact some tracheophyte abundance. These impacts vary with growth form of the tracheophytes. The moss layer is altered by both grazing and trampling. Furthermore, the feces and urine benefit the tracheophytes, encouraging their expansion.

## Impact of Ruminants on Bryophytes

### Grazing

A number of studies have indicated that heavy grazing reduces bryophyte and lichen dominance in both oceanic and continental areas (Austheim *et al.* 2007). Such reductions favor the establishment or increase of more resistant bryophytes such as *Dicranum* (Figure 11) species and members of the large mosses in the *Polytrichaceae* (Figure 5) (Helle & Aspi 1983; Väre *et al.* 1996; Virtanen 2000; Olofsson *et al.* 2004).

Hanley (1982) considered food selection by ungulates to involve four morphological parameters:

1. body size
2. type of digestive system (caecal or ruminant)
3. rumino-reticular volume to body weight
4. mouth size.

They considered large ungulates and caecal digesters to be limited by time compared to small ungulates and ruminant digesters. The high **rumino-reticular** (part of a cow's four stomachs) volume to body weight ratio adapts them to gaining nourishment from plants such as graminoids with thick cell walls and high cellulose content. Conversely, a low rumino-reticular volume to body weight ratio adapts those animals to thriving on browse plants (leaves, twigs, or other high-growing vegetation) with thin, lignified cell walls.





Figure 11. *Dicranum scoparium*, in a genus favored by heavy grazing. Photo by Michael Becker, through Creative Commons.

Milchunas and Noy-Meir (2002) suggest that such environments as cliffs and other small geological formations that prevent herbivory are likely to have greater diversity. They found that 86% of studies in small refuges indicated positive effects of these refuges on plant diversity, whereas only 50% of large refuges had such an impact.

Takala and coworkers (2012) demonstrated the importance of reestablishing herbivory to restore bryophyte communities that were familiar from the days of pasturing large herbivores in the area. They identified three of these restored bryophyte species as suitable indicators of "valuable" grassland habitats: *Abietinella abietina* (Figure 12), *Climacium dendroides* (Figure 13), *Syntrichia ruralis* (Figure 14). In addition, *Rhytidiadelphus squarrosus* (Figure 15) is indicative of rich soil and survives at least moderate grazing (Ingerpuu *et al.* 1998).



Figure 12. *Abietinella abietina*, a moss indicator of valuable grassland habitat. Photo by Hermann Schachner, through Creative Commons.



Figure 13. *Climacium dendroides*, an indicator of valuable grassland habitat. Photo by Krzysztof Ziarnek, through Creative Commons.



Figure 14. *Syntrichia ruralis*, an indicator of valuable grassland. Photo by David T. Holyoak, with permission.



Figure 15. *Rhytidiadelphus squarrosus* growing among grasses where it seems to benefit from grazing. Photo by Johan N., through Creative Commons.

On the other hand, van der Wal and Brooker (2004) demonstrated that in the High Arctic, mosses can mediate the impact of grazers on the abundance of grasses through their effects on soil temperature.



White-tailed deer (*Odocoileus virginianus*; Figure 16-Figure 17) is among a number of ungulates that have a strong impact on the vegetation in its habitat (Rooney & Waller 2003). Herbivory can cause trophic cascades and even modify the physical structure of the habitat. In the Great Lakes region of North America and elsewhere, the white-tailed deer has experienced population surges due to the annihilation of its natural predators. In response, herb diversity is declining while grasses, sedges, and some ferns are increasing. We can expect that these changes will eventually impact the bryophyte communities (Rooney 2009).



Figure 16. White-tailed deer (*Odocoileus virginianus*) lying down. Photo through Creative Commons.



Figure 17. White-tailed deer (*Odocoileus virginianus goudotii*), a rapidly multiplying species with no natural enemies. Photo by Petruss, through Creative Commons.

Peatlands (Figure 18) seem to be especially susceptible to damage from large herbivores (Bleasdale 1998). The white-tailed deer (*Odocoileus virginianus*; Figure 16-Figure 17), in particular, often enters ombrotrophic bogs and minerotrophic fens in search of food or cover (Pellerin *et al.* 2006). These researchers compared five peatlands (Figure 18) that had been subjected to heavy deer browsing for 75 or more years with five peatlands on deer-free islands. They found that the deer had little impact on cover and species composition in the bogs, but cover of lichens was reduced and that of grasses and sedges increased. But the surface area of bare peat also increased. By contrast, the grazed fens differed significantly from the ungrazed

fens. The floristic composition differed, with plant diversity being greater in undisturbed fens, especially for shrubs, sedges, and liverworts (Figure 29-Figure 31). Dunne and Doyle (1998) documented changes in *Molinia*-dominated (Figure 19) blanket bogs in Ireland, where the impact was caused by Kerry cattle, likewise citing impacts on liverworts.

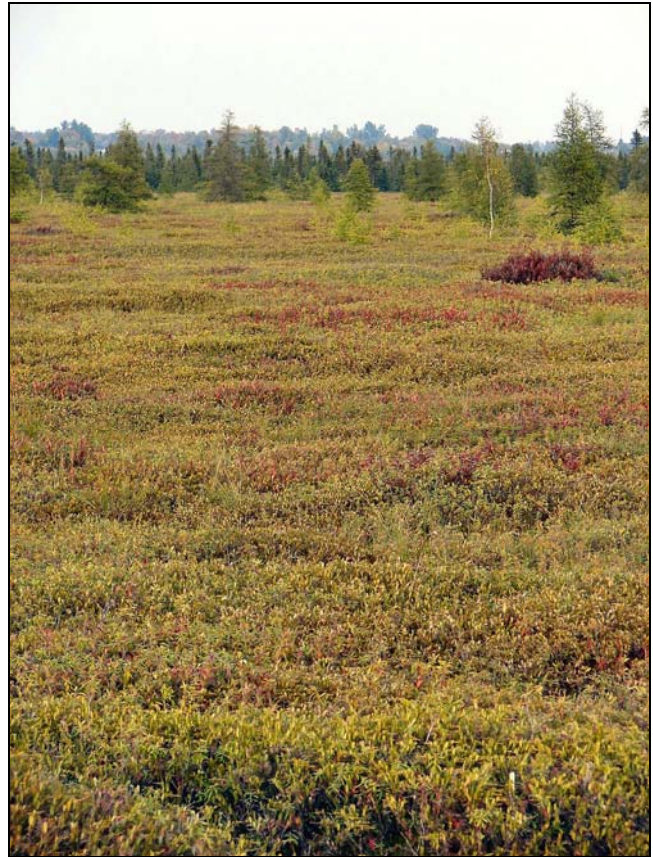


Figure 18. Peatland in Ontario, Canada, a habitat especially vulnerable to browsing and trampling. Photo through Creative Commons.



Figure 19. *Molinia* (= *Melica*) *caerulea* in wetland, a blanket bog species where cattle can change the bryophyte vegetation. Photo by Lamiot, through Creative Commons.

The effects are not the same in all ecosystems. Olofsson *et al.* (2002) used exclosures against herbivores in two Arctic-alpine (Figure 20) plant communities. Exclosures in the snowbed (Figure 21-Figure 22) resulted



in significant biomass increases of both tracheophytes and cryptogams (including bryophytes), but no corresponding changes occurred in the tall herb meadow. The least competition occurred in the open snowbed plots, a condition the researchers attributed to the mammalian herbivores. Excluding the herbivores permits the plant biomass to build up and eliminate the competitive differences.



Figure 20. Arctic landscape. Photo from USFWS, through Creative Commons.

In northwestern Finnish Lapland, Pajunen *et al.* (2008) used exclosures from 1999-2006 to compare the effects of reindeer grazing in a forest-tundra ecotonal area (Figure 21). The area included tundra heath, frost heath, and riparian habitats. They found a general increase in total cover in all exclosures. However, while the dominant tracheophyte groups increased, the bryophytes diminished in both cover and species richness within the exclosures. Like the cattle, it appears that the reindeer maintain a habitat suitable for bryophytes by reducing tracheophyte competition for light.



Figure 21. Forest-tundra ecotones in Rocky Mountain National Park, USA. Photo by Michael Kirsh, through Creative Commons.

Van der Wal and Brooker (2004) investigated the impact of large herbivores on Arctic plant communities (Figure 22-Figure 23), particularly with attention to the impact on the depth of the moss layer. They found that grazing had a domino effect by impacting the depth of the moss layer (Figure 22-Figure 23), subsequently causing a rise in the soil temperature (see Figure 25 for moss effect on soil temperature). That, in turn affected the seed plant abundance and community structure, especially promoting

growth of grasses. The grazing and trampling are both effective in reducing the depth of the moss layer. The grasses benefit not only from the warmer temperatures, but also from the added nutrients from grazer **feces** (poop) and urine.



Figure 22. Moss layer at Nunavut tundra, Northern Canada, showing late snowbed. Photo by A. Dialla, through Creative Commons.



Figure 23. Vegetation in the tundra at Nunavut in the Canadian Arctic Archipelago. Photo by A. Dialla, through Creative Commons.

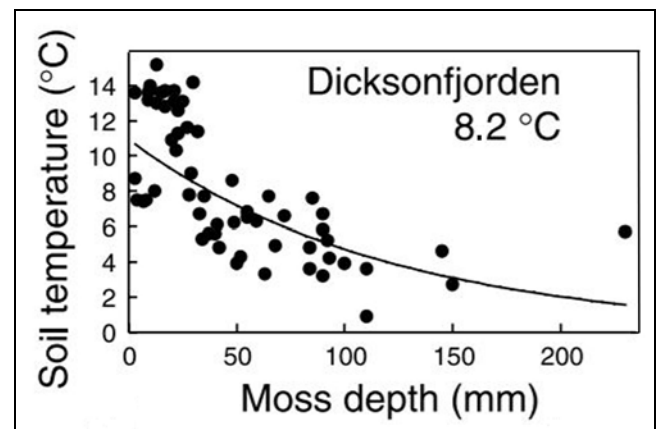


Figure 24. Typical example of moss depth effects on soil temperature in Spitzbergen. Temperature given is ambient temperature at Dicksonfjorden. Modified from van der Wal and Brooker 2004.



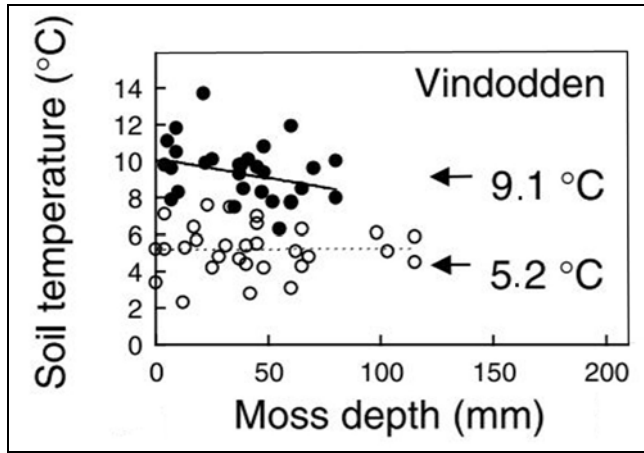


Figure 25. Typical example of moss depth effects on soil temperature at Vindodden in Spitzbergen. Dark and open circles represent two different days with different ambient air temperatures, as indicated. Modified from van der Wal and Brooker 2004.

Similarly, Elkington (1981) found that sheep and rabbit enclosures on limestone grasslands (Figure 26) in Teesdale, England, caused the grassland structure to become more open, largely through the loss of the grass *Festuca ovina* (Figure 27) and reduction of bryophyte and lichen cover. In Utah, USA, the cryptogamic crust (Figure 28) suffered "considerably" from domestic grazing (Anderson *et al.* 1982a, b). In this sensitive ecosystem, the cryptogamic cover was able to recover in 14-18 years.



Figure 26. Limestone grassland in Swindale Wood, England. Photo by Andrew Curtis, through Creative commons.

Porley and Rose (2001), being bryologists, expressed regret that the liverwort mat (*Scapanietum asperae*; Figure 29-Figure 39) was disappearing in English chalklands, dropping from 30 known localities 50 years earlier to 8 or fewer. These communities consisted of the bryophytes *Scapania aspera* (Figure 29), *Frullania tamarisci* (Figure 30), *Porella arboris-vitae* (Figure 31), *Hypnum lacunosum* (Figure 32), *Ctenidium molluscum* (Figure 33), *Dicranum scoparium* (Figure 11), *Pseudoscleropodium purum* (Figure 34), *Calliergonella cuspidata* (Figure 35), *Neckera crispa* (Figure 36), *Homalothecium lutescens* (Figure 37), and occasionally *Ditrichum gracile* (Figure 38) and *Tortella tortuosa*

(Figure 39). These communities have suffered from release from grazing, being replaced by other species. The loss for bryologists is supported by the absence of these communities on the continental chalklands and the conservation importance of the community.



Figure 27. *Festuca ovina* var. *glauca*, a grass lost to grazing in limestone grasslands. Photo by David J. Stang, through Creative Commons.



Figure 28. Cryptogamic crust in Hovenweep National Monument (in Colorado and Utah). Photo from NOS, through Creative Commons.



Figure 29. Leafy liverwort, *Scapania aspera*, dominant species in the liverwort mat (*Scapanietum asperae*). Photo by Hermann Schachner, through Creative Commons.





Figure 30. *Frullania tamarisci*, a leafy liverwort member of the liverwort mat in English chalk grasslands. Photo from Proyecto Musgo, through Creative Commons.



Figure 31. *Porella arboris-vitae*, a leafy liverwort member of the liverwort mat in English chalk grasslands. Photo by J. C. Schou, with permission.



Figure 32. *Hypnum lacunosum*, a moss member of the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.



Figure 33. *Ctenidium molluscum*, a moss member of the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.



Figure 34. *Pseudoscleropodium purum*, a moss member of the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.



Figure 35. *Calliergonella cuspidata*, a moss member of the liverwort mat in English chalk grasslands. Photo by David T. Holyoak, with permission.





Figure 36. *Neckera crispa*, a moss member of the liverwort mat in English chalk grasslands. Photo by Uniprot, through Creative Commons.



Figure 37. *Homalothecium lutescens*, a moss member of the liverwort mat in English chalk grasslands. Photo by David T. Holyoak, with permission.



Figure 38. *Ditrichum gracile*, a moss that sometimes occurs in the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.



Figure 39. *Tortella tortuosa*, a moss that sometimes occurs in the liverwort mat in English chalk grasslands. Photo by David T. Holyoak, with permission.

As late as 1997, Bullock and Pakeman voiced concerns over the effects of reintroducing grazing to lowland heath (Figure 40) in England, citing the lack of information to guide management in these ecosystems. They found that introducing grazing or increasing stocking rates caused a general increase in plant species richness, grass, forb, bryophyte, and lichen cover, and area of bare ground. At the same time, litter depth and cover of dwarf shrubs and scrubs.



Figure 40. Lowland heath in England, a habitat that suffers from the effects of over-grazing. Photo by Roger Key, with permission.

One source of understanding the impact of browsers is through introductions. The Sitka black-tailed deer (*Odocoileus hemionus sitkensis*; Figure 41-Figure 42) to Haida Gwaii in the Queen Charlotte Islands, BC, Canada, in the late 19th Century provided such an opportunity (Stockton *et al.* 2005). The temperate rainforest is a habitat where little information exists on the impact of herbivory by large mammals. This system fortunately gave us a time table because among the 7 islands, there was representation of no deer, deer for less than 20 years, and deer for more than 50 years. When the deer were introduced, their natural predators (wolves and cougars) were absent. Where deer were never present, lower vegetation cover exceeded 80%, whereas it was less than 10% on islands that had



experienced deer browsing for more than 50 years. Interestingly, species richness was similar on all 7 islands, whereas diversity at the plot scale (314 m<sup>2</sup>) was 20-50% lower on islands with more than 50 years of deer browsing. Hence, the deer have simplified the ecosystem. This raises the question of the effects on bryophytes in this temperate rain forest. Typically, bryophyte cover is high, and the forests on Queen Charlotte Island are draped in bryophytes (Figure 43) (*e.g.* Hong & Glime 1997).



Figure 41. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), a species that has devastating effects on vegetation on some islands among the Queen Charlotte Islands, British Columbia, Canada. Photo by D. Gordon E. Robertson, through Creative Commons.



Figure 42. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*). Photo by Wanetta Ayers, through public domain.



Figure 43. Hoh rainforest, with epiphytes on maples, a scene similar to that on the nearby Queen Charlotte Islands. Photo by Kevin Muckenthaler, through Creative Commons.

Contrary to many of these studies, Suominen *et al.* (1999) demonstrated in two Swedish pine forests (Figure 44) that moss cover was higher in unbrowsed plots (by moose, *Alces alces*; Figure 45), and lichen cover was higher in browsed plots. They considered this difference to be a response to the differences in the amount of light reaching the forest floor. In the greater light, the drought-resistant lichens could outcompete the shade-tolerant mosses, reaffirming the differences in response between habitats. Invertebrates differed as well, with higher numbers in unbrowsed plots, but diversity was higher in the browsed plots. This is an aspect that has not been examined relative to bryophyte communities of invertebrates. It also raises the question of the impact of moose browsing on the epiphytic bryophyte flora. Even if the mosses are not eaten, the higher light and lower moisture levels caused by browsing on trees could have an impact.



Figure 44. Pine forest in Sweden. Photo from Pixabay, through Creative Commons.



Figure 45. *Alces alces* bull moose grazing among shrubs. Photo from Denali National Park, Alaska, USA, through Creative Commons.

Brotherson *et al.* (1983) examined the long-term effects of grazing on **cryptogamic crusts** (bryophytes, lichens, algae, and bacteria; Figure 28) in the Navajo National Monument, Arizona, USA. They found that grazing over 40 years had greatly impacted both the



**tracheophyte** (plants with lignified vascular tissue) and cryptogamic communities. The cryptogamic community suffered the most, exhibiting the greatest reduction in cover. Algae were much more tolerant than the lichens and bryophytes. In Idaho, Hilty *et al.* (2004) suggested that following fire in these rangelands, a resting period from livestock grazing would reduce invasive grasses and benefit the native mosses.

Not surprisingly, air pollution, in particular nitrogen pollution, plays a role in the relationship of grazing and bryophytes. Van der Wal *et al.* (2003) found that as livestock grazing increased concurrently with increased N deposition, large-scale degradation of both natural and seminatural ecosystems occurred. Using an experimental approach, these researchers demonstrated that the interplay between grazing and N deposition has led to the replacement of moss-dominated habitats by those dominated by grasses and sedges.

### Trampling

Even when large mammals don't eat bryophytes, they can impose serious damage through trampling (Figure 46). Liddle (1997) considered mosses to be particularly sensitive to disturbances such as trampling. Thus, when trampling is reduced, we should expect bryophyte abundance to increase (Jónsdóttir 1991; Økland 1997; van der Wal *et al.* 2003). But the response is not quite so simple, because it also depends on the response of the rodent community (Austrheim *et al.* 2007). This trampling effect becomes most important in sensitive, slow-growth ecosystems such as those in the Arctic (Callaghan *et al.* 2001).



Figure 46. Introduced reindeer on South Georgia, Ocean Harbour, showing how hoofs could kick up and trample the vegetation. Photo by Roger S. Key, with permission.

In addition to trampling, some hoofed mammals such as roe deer (*Capreolus capreolus*; Figure 47) scrape the ground (Figure 48), dislodging the bryophytes and often exposing bare ground (Clément & Touffet 1981).

Although the role in destruction creates a major impact, trampling and scraping (Figure 1) can at times facilitate dispersal of bryophytes. Péntes-Kónya (2003) documented the role of disturbance in dispersal of the cushion moss, *Leucobryum juniperoideum* (Figure 49), in the Bükk Mountains of northern Hungary where it is the

dominant bryophyte on the ground. Both deer (*Cervidae*) and mouflons (*Ovis orientalis orientalis*, a subspecies of wild sheep) are instrumental in turning over whole cushions during the extremely dry spring. But *L. juniperoideum* actually benefits somewhat from this behavior. It responds to the change in light direction and gravitational pull by growing in a ball (Figure 50). And it has **caducous** (able to break off) leaves that behave like gemmae for reproduction (Figure 51).



Figure 47. Roe deer (*Capreolus capreolus*) male and female. Photo by Juan Lacruz, through Creative Commons.



Figure 48. Roe deer (*Capreolus capreolus*) tracks, indicating the depth of penetration of hooves. These same hoofs can carry bryophyte fragments and "plant" them elsewhere. Photo by James K. Lindsey, with permission.



Figure 49. *Leucobryum juniperoideum*, a species that forms a ball and grows on the new upper side when turned over by disturbance. Photo by David T. Holyoak, with permission.





Figure 50. *Leucobryum juniperoideum* cushion that has been turned upside down and experienced new growth on its new top side. This ball-shaped form is typical after such disturbance. Photo courtesy of Erika Péntzes-Kónya.



Figure 51. Leaf of *Leucobryum juniperoideum* that was turned to under side of clump, showing the development of rhizoids. Photo courtesy of Erika Péntzes-Kónya.

While the stems of *L. juniperoideum* are upside down, rhizoids form on the leaf tips (Figure 51). These plants, and their detached tips, form new plants and can be dispersed by the hooves. Even the leaf lamina cells can produce filaments when the plants are turned over (Figure 52). Nevertheless, during the dry season the disturbance is greater than the regeneration. The new growth occurs faster in the rainy periods. *Leucobryum glaucum* (Figure 53-Figure 54) has similar behavior when turned upside-down (Erika Péntzes-Kónya, Bryonet 13 June 2011).

But cryptogamic crusts (Figure 28) are not so fortunate (Anderson *et al.* 1982b). Domestic grazing greatly reduces the lichens, mosses, and algae forming the crusts. This destruction coincides with soils with heavier texture and greater salinity. Recovery seems to be moderately fast, with crusts usually becoming re-established within 14-18 years.

In three sagebrush communities (Figure 55) in east-central Idaho, USA, cryptogamic crusts (Figure 28; Figure 55) are important in maintaining the ecosystem (Kaltenecker *et al.* 1999). These biological crusts typically

have bryophytes that help to retain water and collect it from dew. Following ~10 years of enclosure to browsing, the crust doubled compared to areas where browsing continued. However, in the area of low sagebrush (*Artemisia arbuscula*; Figure 56), there was the least crust cover and this cover did not differ in exclusion areas there, apparently limited by the gravelly soil surface and dominance of rhizomatous grasses.

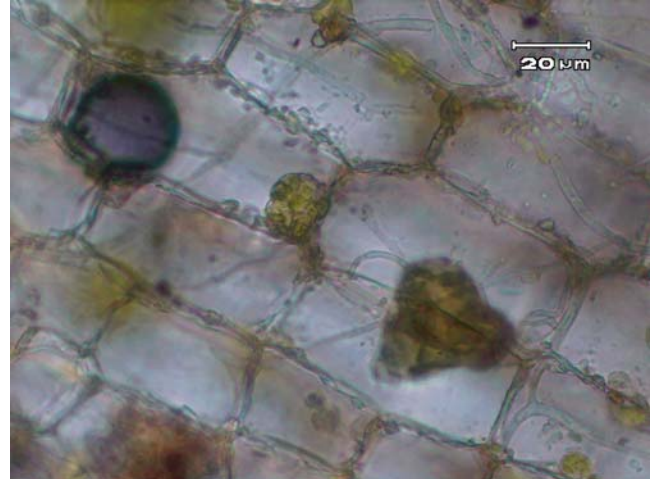


Figure 52. Green cells of *Leucobryum juniperoideum* that developed filaments when moved to the top of the clump. Photo courtesy of Erika Péntzes-Kónya.



Figure 53. *Leucobryum glaucum* in Epping Forest. Photo by Barry Samuels, with permission.



Figure 54. Cushion moss (*Leucobryum glaucum*), a species that forms a ball and grows on the new upper side when turned over by disturbance. Photo by Rob Routledge, through Creative Commons.





Figure 55. Sagebrush steppe in Grand Teton National Park, USA. Photo by Matt Lavin, through Creative Commons.



Figure 56. *Artemisia arbuscula*, a sagebrush in areas where cryptogamic crusts are limited. Photo by Matt Lavin, through Creative Commons.

Yet another response to trampling can be found in fens (Figure 57) (Stammel & Kiehl 2004). Low light availability limits seed germination, accompanied by litter accumulation and competition by mosses.



Figure 57. Fen, sometimes referred to as a flow-through bog. Photo through Creative Commons.

## Manuring

We use manure (Figure 58) to fertilize crops, so it is reasonable to ask what effect ruminant manure has on the one-cell-thick moss leaves. Vanderpuye *et al.* (2002) examined the effects in the *Luzulion nivalis* (Figure 59) snowbeds (Figure 60 at Sassendalen, Svalbard. This location has a low water table, whereas moss tundras usually have no standing water. In these cold environments, manure seems to explain the moss tundra vegetation. The mammals contributing this manure are non-migratory Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7).



Figure 58. Manure-straw mix to be used in agriculture. Photo by Malene Thyssen, through Creative Commons.



Figure 59. *Luzula nivalis*, the species for which the *Luzulion nivalis* is named. Photo by Jeffery M. Saarela, through Creative Commons.





Figure 60. Late snowbeds, Great Britain. Photo by Nigel Brown, through Creative Commons.

Several authors have demonstrated that manure from mammalian grazers and enhanced nutrient cycling resulting from grazing can cause an increase in the graminoids and a concurrent decrease in bryophyte abundance in Arctic-alpine tundra (Olofsson *et al.* 2001; Stark *et al.* 2002).

Van der Wal *et al.* (2004) tested the hypothesis that large herbivores manipulate their own food supply by modifying soil nutrient availability. To do this in a Spitzbergen tundra, they added feces of the reindeer *Rangifer tarandus platyrhynchus* (Figure 7) for four years, thus simulating the effect of feces impact by a larger herd. After the third year, the standing crop of grasses had clearly increased in both shoot density and biomass per shoot. At the same time, the increase in feces and grass productivity did not result in increased grazing pressure. The added feces caused an increase in soil microbial biomass carbon and nitrogen, especially under wet conditions that promoted decay rates. Under dry conditions, the grasses benefitted from the fecal additions. On the other hand, the moss layer depth was significantly impacted by the fecal addition. Areas with the greatest soil microbial biomass likewise had the greatest reduction in moss depth. Van der Wal and coworkers suggested that the moss reduction was due to greater decomposition of the mosses by the enhanced microbes. It is common for Arctic seabirds to affect the tundra vegetation, but here the non-migratory Svalbard reindeer have replaced the seabirds and created an intense manuring effect (Vanderpuye *et al.* 2002). This illustrates yet another mechanism by which grazers impact the bryophyte community, especially in the tundra (van der Wal *et al.* 2004). But Vanderpuye and coworkers consider the reindeer manuring to explain the presence of moss tundras in this Spitzbergen landscape where seabird colonies are absent. Perhaps it is all about the size of the herd.

## Life on Manure – Splachnaceae

A discussion of manuring and bryophytes would not be complete without describing the fascinating relationships of the moss family **Splachnaceae** with manure.

While some bryophytes suffer from the manure of reindeer and caribou, others find these to be their most suitable habitat. These dung mosses include, in particular, many members of the **Splachnaceae**. Included are *Aplodon wormskjoldii* (Figure 61), *Splachnum luteum* (Figure 62), *S. sphaericum* (Figure 63), *Tayloria* spp. (Figure 64), *Tetraplodon mnioides* (Figure 65), *T. paradoxus* (Figure 66), and *Voitia hyperborea* (Figure 67) (Steere 1976). See also Volume 1, Chapter 4-9, Adaptive Strategies: Spore Dispersal Vectors.



Figure 61. *Aplodon wormskjoldii* with capsules, an Arctic dung moss. Photo by Taimyr Anabar Fedosov, with online permission.



Figure 62. *Splachnum luteum* in Alaska, a dung moss with its capsules. Photo courtesy of Andres Felipe Baron Lopez.



Figure 63. *Splachnum sphaericum* with capsules, an Arctic dung moss. Photo by Madcowcult, through Creative Commons.





Figure 64. *Tayloria serrata* with capsules, an Arctic dung moss. Photo by Hermann Schachner, through Creative Commons.



Figure 65. *Tetraplodon mnioides* with capsules, a dung moss in the Arctic. Photo by Hermann Schachner, through Creative Commons.



Figure 66. *Tetraplodon paradoxus* with capsules, a dung moss in the Arctic. Photo by Michael Lüth, with permission.



Figure 67. *Voitia hyperborea* with capsules, a dung moss in the Arctic. Photo by Michael Lüth, with permission.

I am most familiar with these mosses on moose droppings. My first experience was spectacular. I was walking along a path on Isle Royale (Figure 68-Figure 69), Michigan, USA. This is the largest island in Lake Superior (Figure 68) and has a large moose (*Alces alces*) population. My student was ahead of me, searching for the *Splachnum rubrum* (Figure 70-Figure 71) he had seen before I arrived. Suddenly an iridescent purplish red caught my eye! My immediate response was "What in the world...IT'S SPLACHNUM!"



Figure 68. Lake Superior, with Isle Royale indicated by the arrow. Photo from NASA, through public domain.



Figure 69. Isle Royale and its associated smaller islands. Photo by Todd VerBeek, through Creative Commons.





Figure 70. Winter moose dung with *Splachnum rubrum* on Isle Royale. Photo by Janice Glime.



Figure 71. *Splachnum rubrum* capsules on Isle Royale, Michigan. Photo by Janice Glime.

*Splachnum rubrum* (Figure 70-Figure 71) is picky, occupying only the winter dung (Figure 72), the dung that drops as small cylinders. It differs from the large, moist "cow pies" of summer because the winter food consists of twigs and branches and other foods low in nutrients and moisture content.



Figure 72. Moose (*Alces alces*) winter scat. Photo by Cephas, through Creative Commons.

In spring, the capsule odor attracts flies. With luck, the flies have visited another patch of these dung cylinders where *Splachnum rubrum* (Figure 70-Figure 71) has grown and produced capsules. In their mature stage, these capsules smell like dung and attract the flies that subsequently get spores on them. These are transferred to the next patch of dung they encounter. Details of this wonderful family will be provided later in the Habitats volume.

## Cervidae – Deer, Elk, Moose, and Caribou

In the Arctic, members of this family are often dependent on mosses for food, but some members of the family may also impact bryophytes in lower latitudes. Chollet *et al.* (2013) reported that the deer family **Cervidae** has increased in abundance in temperate and boreal forests. The impact of these over-abundant deer is well documented (Kirby 2001), but little is known about the impact on bryophytes (Chollet *et al.* 2013).

### White-tailed Deer – *Odocoileus virginianus*

The white-tailed deer (*Odocoileus virginianus*; Figure 73) has a significant impact on the tracheophyte vegetation, damaging forest vegetation and crops (Horsley *et al.* 2003). Using exclosures (Figure 74), Stewart and Burrows (1989) found that the lichen-moss cover changed little between exclosures and non-exclosures from 1979 to 1985.



Figure 73. *Odocoileus virginianus*, white-tailed deer, seems to have little effect on the bryophyte vegetation. Photo by Scott Bauer, USDA, through public domain.



Figure 74. Exclosures, near for reindeer, far (with young trees) for both rodents and reindeer, at Abisko in sub-Arctic Sweden. Photo by Monteux, through Creative Commons.



In many parts of the eastern USA the increases in deer populations indicate that effects on plant communities may increase in the future (Stromayer & Warren 1997). The impact of heavy deer browsing seems to be particularly exacerbated in swamps by the mossy and soupy peat. Quantitative studies are needed to assess the impact of the white-tailed deer on bryophyte communities.

### Black-tailed Deer – *Odocoileus hemionus*

Chollet *et al.* (2013) compared the impact of browsing by the black-tailed deer (*Odocoileus hemionus*; Figure 75-Figure 76) in two island groups, one with the deer and one without, in the Haida Gwaii archipelago of British Columbia, Canada. In this case, the deer totally avoided browsing, as determined by observations on their feeding. The islands with the black-tailed deer had greater density, cover, and diversity of bryophytes than the islands with no deer. This presumably is due to reduced competition with tracheophytes for light and the total avoidance of foraging on bryophytes by the black-tailed deer.



Figure 75. *Odocoileus hemionus sitkensis*, Sitka Deer, at Haida Gwaii, Vancouver Island, Canada. Photo by D. Gordon E. Robertson, through Creative Commons.



Figure 76. *Odocoileus hemionus sitkensis*, a subspecies found on Vancouver Island, Canada. Photo by Wanetta Ayers, through public domain.

### Reindeer/Caribou – *Rangifer tarandus*

Reindeer and caribou (*Rangifer tarandus*; Figure 77) are different names for the same ungulate in different parts of the world. Their browsing on lichens, especially those

known as reindeer "mosses" (*Cladina* spp.; Figure 78), is well known (Väre *et al.* 1995; Olofsson *et al.* 2004), but their consumption of bryophytes is less well understood.



Figure 77. *Rangifer tarandus* (caribou) grazing. Photo by Peter Nijenhuis, through Creative Commons.



Figure 78. *Cladina* spp. in Tyresta National Park, Sweden – preferred food of reindeer. Photo by Peder Curman, through Creative Commons.

### Importance of Mosses in Diet

Several authors claim that reindeer/caribou seldom eat mosses, despite the limited availability of other foods (Person *et al.* 1980; White & Trudell 1980; Olofsson *et al.* 2004). In a study of food preferences in northern Sweden, Danell *et al.* (1994) found that these animals had a high preference for lichens in winter, but a low one for the common moss *Pleurozium schreberi* (Figure 79). The researchers were unable to explain this difference by nitrogen content, organic matter digestibility, or fiber.





Figure 79. *Pleurozium schreberi*, a common moss often avoided by reindeer and caribou. Photo by J. C. Schou, with permission.

Crête *et al.* (1990) compared lactating caribou in two tundra habitats (Figure 80), one where lichens occupied more than 50% of the ground cover and one where mosses, bare soil, and graminoids dominated the vegetation. The rumen contents reflected the differences in the two habitats. Fewer lichens were eaten in the habitat dominated by mosses and graminoids. Nevertheless, selection for lichens was intense, with lichen cover 25X less but only 1.5-2X less abundant in the rumina.



Figure 80. Barren-ground caribou (*Rangifer tarandus groenlandicus*) grazing in the tundra. Photo from USFWS, through public domain.

Klein (1979) found that the Peary caribou (*Rangifer tarandus pearyi*; ) – a subspecies in the high Arctic islands of Canada's Nunavut and Northwest territories – eat a smaller percentage of lichen than do caribou on the mainland. Rather, they rely on vascular plants and a greater quantity of mosses. Rumen contents contained an average of 58% mosses in Peary caribou of five regions of the Canadian Arctic archipelago during winter, representing five regions (Thomas & Edmonds 1983). Nevertheless, they still prefer the rather scarce foliose lichens in winter (Klein 1979).

In Arctic ecosystems (Figure 81), tracheophyte food can be scarce and mosses subsequently form a major component of the diet of many vertebrate herbivores. In addition to the rodents and birds already discussed in earlier chapters as bryophyte herbivores, ruminants in the Arctic also depend on mosses as a component of their diet. These include reindeer and caribou (*Rangifer tarandus*; Figure 80-Figure 82) and muskox (*Ovibos moschatus*; Figure 83) (Prins 1982; Prop & Vulink 1992; Longton 1997; van der Wal *et al.* 2000; Joly *et al.* 2007).



Figure 81. Arctic tundra from air. Photo by Robert Berdan, with permission.



Figure 82. *Rangifer tarandus pearyi*, a moss eater. Photo by Morgan Anderson, Environment, with online permission.



Figure 83. Muskox (*Ovibos moschatus*), a tundra moss eater. Photo through Creative Commons.



Manseau *et al.* (1996) considered the habitat of caribou (*Rangifer tarandus*; Figure 80) to be very susceptible to both grazing and trampling by the caribou. In fact, it appears that the herd size is regulated by the amount of available forage in its summer range. They found that the lichen mat was absent in grazed areas of the shrub tundra and that those areas were either bare or occupied by fragments of dead lichens and mosses.

On the other hand, lichens are very important to the caribou diet. Pharo and Vitt (2000) reported that in the montane forests of western Canada, the lichens preferred by the endangered woodland caribou (*Rangifer tarandus caribou*; Figure 84) were abundant, but the ground cover was dominated by feather mosses, especially *Pleurozium schreberi* (Figure 79).



Figure 84. Caribou (*Rangifer tarandus caribou*) feeding in tundra, Northwest Territories, Canada. Photo by Robert Berdan, with permission.

The Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) includes coprophagy among its feeding strategies (van der Wal & Loonen 1998). That is, they feed on the feces of barnacle goose (*Branta leucopsis*; Figure 85). In fact, the majority of the reindeer in the research area were seen feeding on these droppings instead of vegetation. The number of goose droppings eaten were enough to supply the daily energy requirements for 68 reindeer. But they were very selective in their choice of droppings, choosing those containing grass and avoiding those with moss fragments. There did not appear to be important differences in nitrogen, phosphorus, magnesium, calcium, sodium, potassium, or energy content between the two types of feces. Fiber, on the other hand, differed between grass- and moss-dominated droppings, with less fiber associated with the mosses. Thus, the grass-dominated droppings were more digestible.

Nevertheless, Arctic herbivores, including *Rangifer tarandus*; Figure 80, Figure 84), do consume substantial quantities of bryophyte biomass (van der Wal & Brooker 2004) and further damage them through trampling. Liddle (1997) has shown that trampling can be particularly destructive to mosses in Arctic ecosystems because of their slow growth rate and recovery (Callaghan *et al.* 2001).



Figure 85. Barnacle goose (*Branta leucopsis*); Svalbard reindeer eat the feces of this goose, but avoid feces with mosses. Photo by Allan Hopkins, through Creative Commons.

### Digestibility

Several authors have attributed the usual lack of consumption to the low digestibility of mosses (Person *et al.* 1980; White & Trudell 1980; Thomas & Kroeger 1981). Nevertheless, on Arctic islands with little lichen availability, the caribou herds eat mosses (Staaland *et al.* 1979).

Robert Pegau, in correspondence with Howard Crum, reported that reindeer in Alaska scarcely digest mosses (Crum 1973), although they do graze on *Polytrichum* (Figure 5), *Aulacomnium turgidum* (Figure 86), and *Hylocomium splendens* (Figure 87) (Bland 1971). A high content of moss (up to 12%) in winter in the rumen of reindeer at Hardangervidda, Norway, may be ingested unavoidably while grazing on lichens (Gaare & Skogland 1975). Lichens, on the other hand, are readily digested (Crum 1973).



Figure 86. *Aulacomnium turgidum* in Norway, a moss species eaten by Alaskan reindeer. Photo by Jutta Kapfer, with permission.





Figure 87. *Hylocomium splendens*, a moss species eaten by Alaskan reindeer. Photo by Rob Routledge, through Creative Commons.

Nevertheless, when lichens are overgrazed, reindeer may turn to mosses. On Svalbard, where desirable lichens are scarce, Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) had a rumen content of 32-39% mosses, hardly an accidental accompaniment to lichens (Reimers 1977). In fact, van der Wal (2006) considers Svalbard reindeer to be moss specialists, consuming up to 54% of their winter diet as mosses, a figure similar to that of Peary caribou (*Rangifer tarandus pearyi*; **Error! Reference source not found.**) in northern Canada (Klein 1979). Rather than eating lichens, reindeer in the High Arctic seem to have replaced lichens as winter forage with bryophytes (Staalnd *et al.* 1983; Staalnd 1986; Longton 1997). Staalnd *et al.* (1983) found that the mosses on Svalbard provided a higher mineral content than the food available in Norway, but at the same time, the mosses had lower digestibility than the lichens and browse in Norway.

In a different study, Bjorkvoll *et al.* (2009) found that the winter diet of Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) was only 22-30% mosses during the three-year period of the study. Effects of snow cover in late winter affected the dietary composition. *Polytrichum* (Figure 5) was the most common bryophyte and comprised a relatively high proportion in the early winter diet.

In the southern Northwest Territories, Canada, the barren-ground caribou (*Rangifer tarandus groenlandicus*; Figure 1, Figure 88) included mosses, lichens, and shrubs in its diet (Thomas *et al.* 1984). Using fermentation in ruminal fluids in test tubes, Thomas and coworkers found that the dry matter biomass of shrubs was reduced by 37-51%, whereas the bryophytes were reduced only 7-28%. The lichens averaged 49% reduction in 180 hours. In a different case, Thomas and Kroeger (1981) examined *in vitro* digestion in ruminal fluids from *Rangifer tarandus groenlandicus* that had been shot in its winter range in southern Northwest Territories, Canada. This animal had poor digestion (15-27%) of two species of mosses and a liverwort.

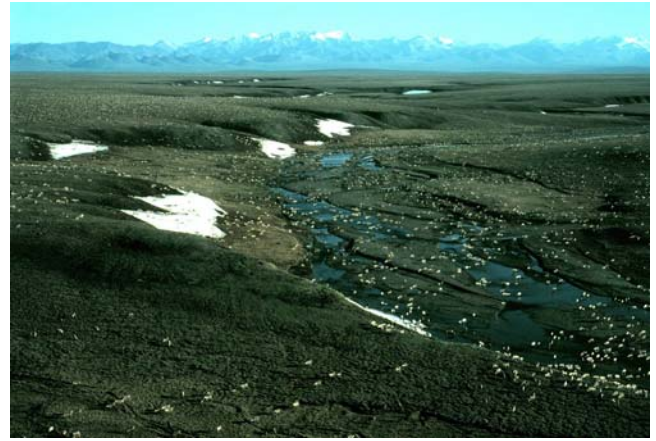


Figure 88. Barren-ground caribou (*Rangifer tarandus groenlandicus*) herds. Such numbers cause considerable damage to the vegetation, including bryophytes. Photo from U.S. Fish and Wildlife, through public domain.

In Aoluguya, Great Khingan Mountain Range of Inner Mongolia, Feng and Bai (2011) examined factors related to bryophyte consumption and digestion. The bryophytes have high concentrations of acid-detergent fiber, making them indigestible. This raises the question, what permits some reindeer to subsist largely on bryophytes, especially in winter?

Staalnd and coworkers (1979) suggest that the reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) on Svalbard may be adapted to eating mosses. These reindeer have an enlarged caecum-colon complex that appears to be an adaptation to a bryophytic diet by using the assistance of bacteria. These reindeer also have a high number of fiber-digesting rumen bacteria (Orpin *et al.* 1985), facilitating digestion. The rumen bacteria of the Svalbard reindeer are very effective in facilitating fiber digestion and nitrogen metabolism, providing an important adaptation for living in high Arctic habitats with poor nutritional conditions.

The Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) eat mosses in the winter because they are unable to migrate to forested lichen habitat (Longton 1992). Nevertheless, digestibility of mosses by these caribou is typically low, only 11-35% in summer and 3-11% in winter (Thomas & Kroeger 1980). Thus, one must ask just what the mosses provided for the animals. If ruminants, with their massive digestive bacteria flora, are unable to digest the mosses, one would assume they would be even less digestible for most other large mammals. There are likely to be other populations with similar winter grazing problems. Callaghan *et al.* (2004) considered deep snow to be a deterrent from winter grazing in some Arctic areas in some years. Areas of deep snow could force these ruminants into lower elevations or lower latitudes and prevent them from finding enough of the desired winter food source of lichens.

If mosses are difficult to digest and provide limited nutritional value, why are they heavily consumed in the Arctic? Ardea and Sage (1982) claim that the reindeer must consume 7 kg of mosses to extract the same energy they would get from just 0.5 kg of tundra grass.

We have seen that Prins (1982) suggested that they eat mosses for their arachidonic acid because of its ability to remain flexible in winter. These acids are major constituents of animal fats, especially in phospholipids of



cell membranes (Ardea & Sage 1982). These make the membranes more fluid, especially at the low temperatures of winter.

Feng and Bai (2011) added to the arachidonic acid possibilities. Reindeer are not able to synthesize arachidonic acid, but that which is ingested can provide several benefits to them. This acid is a precursor for some prostaglandin hormones, it has a low melting point that could lower the freezing point of the reindeer extremities, and it provides protection to cell membranes in the cold.

### Effects on Soil Temperature

In the wet meadow vegetation of Barrow, Alaska, USA, Miller *et al.* (1980) found that in exclosures (Figure 74) the moss increased and the thaw depth decreased, suggesting that the mosses insulated the permafrost (Figure 89) against warming, and thus against thawing. Van der Wal and Brooker (2004) examined effects of reindeer herbivory on a moss layer of *Sanionia uncinata* (Figure 90), *Tomentypnum nitens* (Figure 91), and *Aulacomnium* spp. (Figure 92). Moss depth in the grazed controls was  $38 \pm 6$  mm compared to  $57 \pm 10$  mm in the ungrazed exclosures. Furthermore,  $\text{NH}_4\text{-N}$  was considerably lower inside the exclosures, but nitrogen mineralization potential was reduced by greater moss depth. A 10-cm-thick mat of mosses causes  $\sim 4.4^\circ\text{C}$  drop in soil temperature, with the temperature decreasing with moss depth (Figure 93). Manipulating the soil temperature had no effect on moss growth, but the grass *Poa arctica* and flowering plant *Cardamine nymmanii* (Figure 94) both were reduced by 50% biomass in the chilled soils (van der Wal *et al.* 2001). These temperature decreases not only affect roots and rhizomes of tracheophytes, but they also affect decomposer communities by affecting the soil microbes and consequently affecting nutrient cycling (Harrison & Bardgett 2008).



Figure 90. *Sanionia uncinata*, a moss species affected by reindeer grazing. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

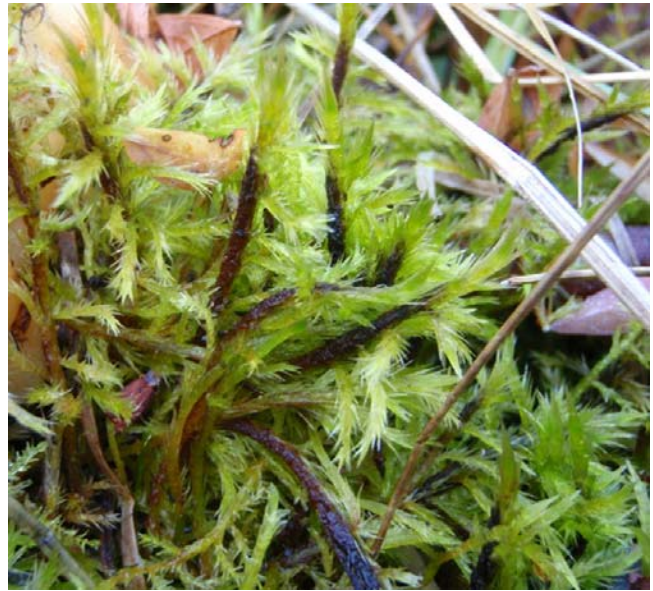


Figure 91. *Tomentypnum nitens*, a moss species affected by reindeer grazing. Photo by Scot Loring, through Creative Commons.



Figure 89. Digging in permafrost in the tundra, using a jackhammer. Photo by Nick Bonzey, through Creative Commons.



Figure 92. *Aulacomnium palustre*, a moss species affected by reindeer grazing. Photo by Kristian Peters, through Creative Commons.



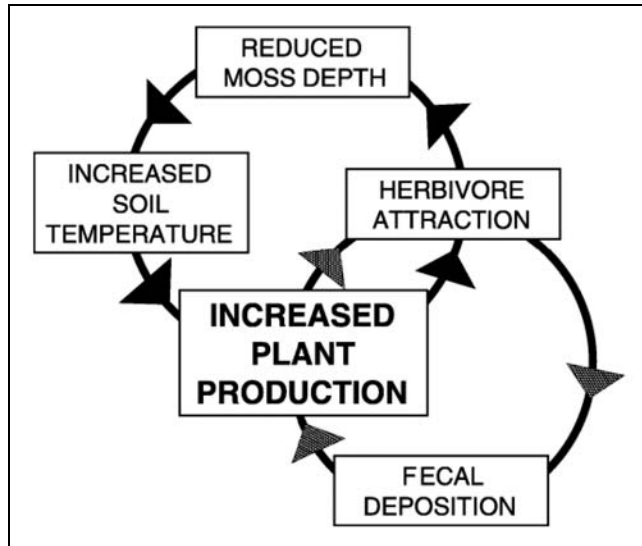


Figure 93. Relationship of mosses, herbivores, and soil temperature as conceptualized by van der Wal and Brooker 2004.



Figure 94. *Cardamine nymanii* in flower in Spitzbergen, a food much eaten by ruminants in Alaska. Photo by Bjoertvedt, through Creative Commons.

### Microbial Responses to Grazing

Väre *et al.* (1996) found that microbial activity was significantly depressed at sites grazed by reindeer. This seems to be the result of reduced soil moisture at the grazed sites, especially during dry periods. Furthermore, grazing reduced the levels of all exchangeable nutrients by 30-60% in the organic layer of the soil. These factors contributed to the reduction of fine roots.

### Temporal Differences

Both food choice and digestibility vary by season. Thomas and Kroeger (1980) found summer digestibility of mosses to range 11-35%, whereas winter digestibility ranged only 3-11%.

Thompson and McCourt (1981) studied the phenology of diet in the porcupine caribou herd (*Rangifer tarandus granti*; Figure 95) in the northern Yukon. The winter diet was dominated by lichens (66.7%) with most of the remainder being mosses (28.8%). In summer they shifted to primarily tracheophytes, especially sedges in spring, but shrubs dominated (>98%) after calves were born. The diet of shrubs declined and lichens again became prominent beginning in August.



Figure 95. Porcupine caribou (*Rangifer tarandus granti*) grazing. Photo by Dean Biggins, through public domain.

In the Great Khingan Mountain Range of Inner Mongolia, bryophyte consumption by reindeer also varied by season (Feng & Bai 2011). In April bryophytes comprised 5.63% of the feces, dropping to 2.2% in June, and rising to 12.9% in September. The four most common genera of bryophytes were *Pleurozium* (Figure 79), *Dicranum* (Figure 11), *Aulacomnium* (Figure 86, Figure 92), and the leafy liverwort *Ptilidium* (Figure 96). *Pleurozium schreberi* (Figure 79) comprised over 70% of the bryophyte total. But some seasonal differences are present. *Polytrichum juniperinum* (Figure 97) only occurred in large amounts in September. Despite the seasonal changes in amount of bryophytes eaten, the relative proportions among the other bryophyte species did not change appreciably between seasons. Nevertheless, sampling of the dominant forest floor bryophytes revealed that the reindeer are selective. *Hylocomium splendens* (Figure 87), *Sphagnum* spp. (Figure 98), and *Pleurozium schreberi* (Figure 79) are dominant bryophytes in the four types of forests investigated, but of these only *Pleurozium schreberi* was eaten. Additionally, *Didymodon* (Figure 99) and *Racomitrium* (Figure 100) occurred only occasionally in the feces.



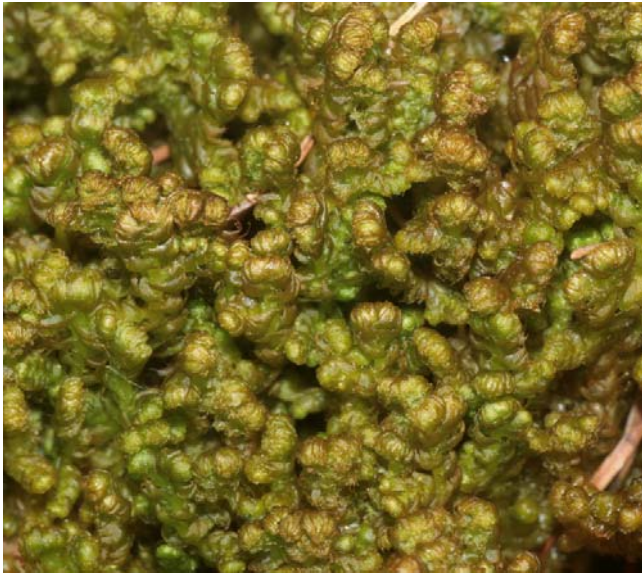


Figure 96. *Ptilidium ciliare*, leafy liverwort in a genus that is one of the four most common bryophytes in the reindeer grazing grounds of the Great Khingan Mountain Range of Inner Mongolia. Photo by Hermann Schachner, through Creative Commons.



Figure 97. *Polytrichum juniperinum*, a moss species that occurred in its greatest amounts in reindeer feces in September in the Great Khingan Mountain Range of Inner Mongolia. Photo by Janice Glime.



Figure 98. *Sphagnum austini*, a dominant moss in Mongolian reindeer habitats, but was not eaten by them. Photo by Michael Lüth, with permission.



Figure 99. *Didymodon rigidulus* var *icmadophilus*, member of a genus that is occasionally consumed by reindeer in the Great Khingan Mountain Range of Inner Mongolia. Photo by Michael Lüth, with permission.



Figure 100. *Racomitrium* in grey-green mounds, a genus that occasionally is consumed by Mongolian reindeer. Photo by Manfred Morgner, through Creative Commons.

In the five regions studied, Thomas and Edmonds (1983) found that monocots and mosses comprised 13% and 58%, respectively, of the rumen content of Peary caribou (*Rangifer tarandus pearyi*; Figure 6) in the Canadian Arctic archipelago. However, the digestibility of mosses for caribou is low, with the summer digestibilities of mosses ranging 11-35%, whereas lichens range 18-86% (Thomas & Kroeger 1980, 1981). In winter the mosses drop to 3-11% digestibility, suggesting they are not being consumed primarily for their nourishment. Perhaps it fools the caribou into "thinking" that they are full.

Thomas *et al.* (1984) also found that the dry matter disappearance of 22 plant species was significantly higher in March of 1981 than in tests performed one year earlier. The variation in the ruminal fluids coincided with differences in the physical condition of the caribou, which may have resulted from their nutritional history.

#### Site Differences

Based on these observations, we can expect the diet to differ by location. Pearce (1997) found that in the Kara area of Russia, 14% of the moss sites and 10% of the lichen sites experienced severe damage from reindeer activity. On



the other hand, in Norway, 73% of the moss sites and 85% of the lichen sites suffered from grazing and trampling. The reindeer populations of Norway had doubled in the previous years, resulting in soil erosion in 75% of the sites. Only 8% of the Russian sites suffered from erosion.

Sørmo *et al.* (1999) examined fragments in the rumen of Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) in the western parts of Spitsbergen at Nordenskiöld where tundra vegetation is somewhat abundant and on the island of Nordaustlandet where they live in a polar desert with scarce vegetation. On Nordenskiöld the rumen contents were primarily mosses and grasses, whereas on Nordaustlandet they were primarily the flowering plants *Saxifraga* spp. (Figure 101).



Figure 101. *Saxifraga cespitosa* on Svalbard. This genus is the primary food of the Svalbard reindeer on Nordaustlandet. Photo by Victor M. Vicente Selvas, through Creative Commons.

### Grazing Effects on Bryophytes and Vegetation

Van der Wal (2006) considered the ruminant herbivores to cause predictable changes in the ecosystem vegetation. Van der Wal points out that reindeer can deplete the lichens and switch to mosses (Staaland *et al.* 1993) with no detrimental effects to the reindeer population (Cooper & Wookey 2001). In fact, the carrying capacity for large ungulates increases when the vegetation switches to mosses, and increases again when it converts to grasses after extensive herbivory on mosses. A similar succession from lichens to mosses to graminoids is known where caribou (reindeer) range in Greenland (Thing 1984), Russia (Vilchek 1997), North America (Palmer & Rouse 1945; Klein & White 1987; Manseau *et al.* 1996), Fenno-Scandia (Helle & Aspi 1983, Gaare 1997), and the high arctic islands (Van der Wal *et al.* 2001). Even domesticated reindeer in boreal forest ecosystems cause the conversion of lichen vegetation to mosses (Väre *et al.* 1996; Mäkipää 1998). And in Norway the moss-dwarf shrub heath gives way to grass domination under the pressure of reindeer grazing (Olofsson *et al.* 2001, 2004). Thing (1984) interpreted this progression of species as ecosystem damage.

Sarvas (1937) found that mosses like *Polytrichum juniperinum* (Figure 97) can survive feeding and trampling because they have rhizomes and rhizoids that can survive

the above-ground feeding. These underground parts are able to germinate and form new plants. Oksanen (1978) found that *Polytrichum hyperboreum* (Figure 102) in northern Norway is very resistant to trampling by reindeer. It is likely that *Polytrichum* species are also dispersed by the reindeer, and some of these are delivered to areas where competition with species of *Cladonia* (Figure 103) is avoided (Helle & Aspi 1983).



Figure 102. *Polytrichum hyperboreum* with capsules, a moss species that is very resistant to trampling. Photo by Kristian Hassel, through Creative Commons.



Figure 103. *Cladonia cornuta*, a member of the lichen genus that competes with the moss *Polytrichum*. Photo through Creative Commons.

Van der Wal (2006) suggests the change in species begins with selection of lichens over mosses, causing greater lichen losses. This change is further promulgated by trampling, which is more damaging to lichens than to mosses, especially when they are dry (Cooper *et al.* 2001). If grazing is suppressed, the system may change back to lichen domination, but the change is slow (Crettenden 2000; Cooper & Wookey 2001; Den Herder *et al.* 2003). In fact, as lichens recover, they may "smother" the mosses (Gaare 1997; Van der Wal *et al.* 2001). A more likely explanation is the allelopathic effect of the many lichen secondary compounds (Lawrey 1995).

In *Pinus sylvestris* forests (Figure 104) of Fennoscandia, in 50-year-old exclosures indicate that



certain bryophytes benefit from reindeer grazing (Väre *et al.* 1995). This was particularly true for *Dicranum* spp. (Figure 11) and *Pleurozium schreberi* (Figure 79). In heavily grazed sites, the food lichen species *Cladina* spp. (reindeer "moss"; Figure 78) disappears. However, in ungrazed sites, *Cladina* species replace the *Cladonia* (Figure 103) lichen species and small bryophytes like *Barbilophozia* spp. (Figure 105), *Pohlia nutans* (Figure 106), and even *Polytrichum* spp. (Figure 102).



Figure 104. *Pinus sylvestris* (Scots pine) forest with mosses. Photo by Hermann Falkner, through Creative Commons.



Figure 105. *Barbilophozia floerkei*, a leafy liverwort among the species replaced by *Cladina* in ungrazed sites. Photo by Hermann Schachner, through Creative Commons.



Figure 106. *Pohlia nutans* in Svalbard, among the moss species replaced by the lichen *Cladina* in ungrazed sites. Photo by Michael Lüth, with permission.

Virtanen (2000) used exclosures to determine the effects of herbivory on vegetation of a mountain snowbed in northwestern Finland. Unlike Sarvas (1937) and Oksanen (1978), Virtanen found that the dead plant material of *Polytrichaceae* (Figure 97, Figure 102) in the 15-year exclosures had increased; the moss *Kiaeria* (Figure 107) had disappeared. His results contradicted the assumption of other researchers that herbivory was unimportant in areas of low productivity. In these snowbeds, it clearly had an impact.



Figure 107. *Kiaeria starkei*, a moss species that disappears in exclosures. Photo by Hermann Schachner, through Creative Commons.

Olofsson *et al.* (2001) examined the effects of summer grazing on the tundra heath vegetation in northern Norway. Comparing winter grazed, lightly summer grazed and heavily summer grazed vegetation at four different sites. They concluded that the highest productivity occurs at intermediate grazing pressure. They found that intensive grazing may be responsible for the transition from a moss-rich heath tundra to a productive grass-sedge-dominated steppe-like tundra vegetation. Intermittent grazing can actually enhance summer productivity.

In the sub-Antarctic on South Georgia, experimental reindeer exclosures demonstrated the changes to the vegetation after 1 year (Leader-Williams *et al.* 1987). Native grasses (*Poa flabellata*; Figure 108) and dwarf shrubs (*Acaena magellanica*; Figure 109) increased in response to the absence of grazing. The moss *Polytrichum* (Figure 97, Figure 102) likewise increased, but to a lesser extent. This is reminiscent of the responses in rodent exclosures (see Chapter 17). Macrolichens showed little change, as did moss-bank communities. The lichen cover is likely to require decades to recover.

Using approximately 3000 permanent plots in Finland and more than 10,000 plots in all in three different surveys, Mäkipää and Heikkinen (2003) measured changes in the vegetation. During this time, the forest floor moss *Hylocomium splendens* (Figure 87) decreased in abundance while *Dicranum polysetum* (Figure 110) increased. In the northern part of Finland, grazing by semi-domestic reindeer coincided with a decline of *Cladina* (Figure 78) lichens, a favorite food, while the mosses *Dicranum* spp. increased. *Polytrichum juniperinum* (Figure 97), *Pohlia nutans* (Figure 106), and *Brachythecium* sp. (Figure 113), moss species typical of disturbed sites, increased. *Sphagnum* (Figure 98)



abundance decreased, especially in western Finland where the moss *Pleurozium schreberi* (Figure 79) also was favored.



Figure 108. *Poa flabellata* on South Georgia, a species that increases when grazing stops. Photo by Roger Key, with permission.



Figure 109. *Acaena magellanica*, a shrub that increases when grazing is stopped. Photo by El Grafo, through Creative Commons.



Figure 110. *Dicranum polysetum*, a moss species that increased in permanent plots. Photo by Hermann Schachner, through Creative Commons.

Hansen *et al.* (2007) followed vegetation changes for 26 years following the reintroduction on the northwest coast of Spitsbergen, Svalbard, of the Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7). The population size fluctuated, and when it reached high numbers, it caused a top-down effect on the vegetation that included a decrease in the cover of mosses. The preferred winter forage, fruticose lichens, almost disappeared. When the grazing pressure was relieved, the mosses not only recovered completely, but within six years they exceeded the pre-reindeer levels.

In the Arctic and alpine tundra, reindeer (*Rangifer tarandus*; Figure 77) consume 22-30% of their winter diet as moss (Heggberget *et al.* 2010). These researchers expressed concern that climate change, predictably greater in these northern areas, could compromise the available winter forage. Lichens are likely to be impacted, forcing the reindeer to seek other forage. In some populations, a larger alimentary tract has adapted to the reindeer diet.

### Roe Deer – *Capreolus capreolus*

Several studies have revealed the ability of hoofed mammals to transport bryophyte propagules. One such study demonstrated the epizoochorous dispersal of bryophyte fragments by roe deer (*Capreolus capreolus*; Figure 111) (Heinken *et al.* 2001). They found 106 bryophyte fragments, almost all stem fragments, lodged in the coats and hooves of 15 roe deer and 9 wild boar (*Sus scrofa*; Figure 112). These represented 12 bryophyte species, with the most abundant being *Brachythecium velutinum* (Figure 113), *Hypnum cupressiforme* (Figure 4), and *Eurhynchium hians* (Figure 114). These were typically about 3.6 mm long, but ranged 0.5-35 mm. The species that were most common were slender pleurocarpous mosses (growing horizontally) with erect, acute leaves. Robust acrocarpous mosses (growing upright) that formed tall turfs were generally absent.



Figure 111. Roe deer (*Capreolus capreolus*) male and female, showing the hooves that can transport bryophyte fragments. Photo by Jojo through Wikimedia Commons.

Roe deer can do considerable damage to bryophyte vegetation (Clément & Touffet 1981). Following fire in the Brittany heathlands, roe deer were responsible for bryophyte disappearance due to scraping by roe deer.





Figure 112. Wild boar (*Sus scrofa*), a species that can transport bryophytes in its long hair and on its hooves. Photo by Jerzy Strzelecki, through Creative Commons.



Figure 113. *Brachythecium velutinum*, a moss that is one of the most abundant bryophytes transported by sheep. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 114. *Eurhynchium hians*, one of the most abundant moss species carried by roe deer (*Capreolus capreolus*). Photo by Michael Lüth, with permission.

Bryophytes do not appear to serve as food for this species (Tixier *et al.* 1997). Although they are generalist feeders by using a variety of types of food, they are selective within the food types. Their use of food species correlates negatively with fiber content. Bryophytes were specifically avoided in all seasons. Even so, they preferred plants that had high concentrations of protein-binding

phenolic compounds, leading Tixier and coworkers to suggest that they might have specific mechanisms for deactivating these compounds. For many animals, protein-binding compounds prevent the animals from obtaining nutrition from the proteins they eat, even from accompanying foods that don't have the binding compounds.

### Hog Deer – *Axis porcinus*

In southeastern Australia, both introduced mammals and native species consume plants (Davis *et al.* 2008). Whereas the swamp wallabies (*Wallabia bicolor*; Figure 115) consume the largest proportion of tree browse, the hog deer (*Axis porcinus*; Figure 116) consume the largest proportion of mosses, however only removing less than 0.01%.



Figure 115. *Wallabia bicolor* and large joey. Photo by Peripatus, through Creative Commons.



Figure 116. *Axis porcinus*, a moss consumer. Photo by Brent Huffman, through Creative Commons.

### Summary

Bryophytes and ruminants interact in various ways. Some of these animals eat the bryophytes, particularly reindeer in Arctic regions, and most are capable of creating disturbance that can damage the bryophytes. Trampling and scraping break and dislodge the



bryophytes, but at the same time these activities can contribute to dispersal as the fragments adhere to hooves and fur/hair/wool.

Reindeer/caribou (*Rangifer tarandus*) typically cannot digest bryophytes well, but on Svalbard, where they have no place to go for winter, mosses are a staple in the diet. They seem to have adapted by being able to absorb more of the nutrients from the mosses through an enlarged caecum-colon complex.

Both black-tail (*Odocoileus hemionus*) and white-tail (*Odocoileus virginianus*) deer and roe deer (*Capreolus capreolus*) apparently avoid eating bryophytes.

When grazing is light, it can favor such mosses as *Rhytidiadelphus squarrosus*, *Polytrichaceae*, and *Brachythecium*. Colonizers like *Pohlia nutans* can benefit from disturbance and increased light. Leafy liverworts like *Barbilophozia floerkei* decrease with grazing. But the bryophyte communities depend on the site, with Arctic and alpine communities responding differently from more temperate ones. Rodents likewise can have a profound effect on the bryophytes, with communities responding differently depending on the foraging ruminants present.

Bryophytes suffer from manuring and urine, perhaps due to increased microbial decomposition, or to greater competition from the enriched tracheophytes.

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CHAPTER 18-2

LARGE MAMMALS: RUMINANTS –

NON-CERVIDAE

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TABLE OF CONTENTS

Moschidae – Musk Deer – <i>Moschus</i> .....	18-2-2
Bovidae – Antelopes, Cattle, Gazelles, Goats, Sheep, and Relatives .....	18-2-3
Sheep – <i>Bovis</i> .....	18-2-3
Goats – <i>Capra</i> .....	18-2-11
Cattle – <i>Bos</i> .....	18-2-12
Bison – <i>Bison</i> .....	18-2-14
Summary .....	18-2-15
Acknowledgments .....	18-2-15
Literature Cited .....	18-2-15



# CHAPTER 18-2

## LARGE MAMMALS – RUMINANTS



Figure 1. *Ovis aries* (Soay sheep) resting on mat of mosses and grasses. Their herbivory on grasses can benefit the mosses. Photo from Biopix, through Creative Commons.

### Moschidae – Musk Deer – *Moschus*

Green (1987) found that for Himalayan musk deer (*Moschus chrysogaster*; Figure 5), the choice of mosses as food was highly seasonal and usually avoided. They preferred forbs and woody plants in autumn and winter, positively avoiding bamboo leaves and mosses.

Ihl and Barboza (2007) compared the digestible value of a typical ruminant food for Arctic muskoxen (*Ovibos moschatus*; Figure 2) with that of the mosses *Hylocomium splendens* (Figure 3) and *Tomentypnum nitens* (Figure 4) from two locations in Alaska, USA. First they acclimated the muskoxen to mosses for 15 consecutive days. Using forages from ruminally fistulated muskoxen (having passageway cut from rumen to outside) they determined that ruminal degradation was not affected by previous acclimation to mosses.

Ruminal digestion caused a loss of dry matter during 48 hours of ruminal incubation of grasses (-49%), but mosses actually gained dry matter (44-57%) (Ihl & Barboza 2007). These changes were unaffected by

suspending the forages in the rumen for 15 consecutive days, a procedure that could induce digestive enzymes in response to previously uneaten food sources. The incubated mosses gained 435-680% N and 18% fiber!



Figure 2. *Ovibos moschatus*, a species that does not acclimate to digestion of mosses. Photo by Laurent Bélanger, through Creative Commons.





Figure 3. *Hylocomium splendens*, a species common in the habitat of Arctic musk oxen. Photo from Botany Website, UBC, with permission.



Figure 4. *Tomentypnum nitens*, a species common in the habitat of Arctic musk oxen. Photo by Jutta Kapfer, with permission.

Ihl and Barboza (2007) suggested that the gain in mass by the mosses was due to microbial colonization and adsorption of fibrous particles onto the absorbent mosses. When digested with acid-pepsin, the ruminally incubated mosses lost little nitrogen, whereas the hay lost 23% nitrogen. Ihl and Barboza suspected that winter consumption of mosses may be the result of selecting other plants that grow mixed within the moss community, thus explaining the presence of mosses in feces. The times when mosses occurred in the feces of these animals indicated low availability of preferred foods. As noted in an earlier chapter, Arctic birds likewise experience periods of low availability of desired foods, but their digestive processes differ, so studies on ruminants may not be indicative of digestibility for birds, or *vice versa*.

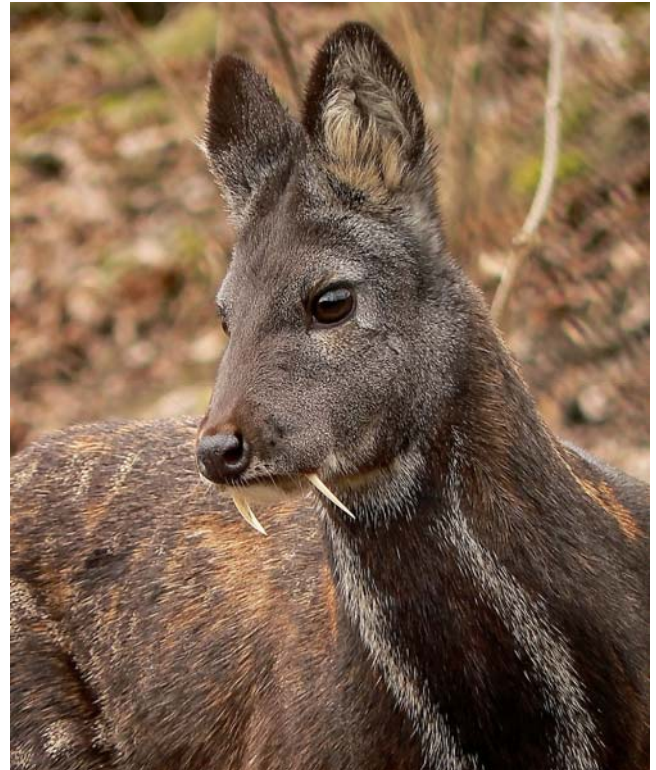


Figure 5. Himalayan musk deer (*Moschus moschiferus*), a species that eats mosses seasonally. Photo by Николай Усик, through Creative Commons.

## Bovidae – Antelopes, Cattle, Gazelles, Goats, Sheep, and Relatives

### Sheep – *Ovis*

Sheep can have a serious impact on the bryophyte communities. Downing (1992) suggested their impact on limestone bryophyte vegetation at Attunga, Australia. Rieley *et al.* (1979) reported that sheep graze in Welsh oakwoods on grasses until ultimately the bryophytes increase in abundance. Austrheim *et al.* (2007) found a similar increase in bryophytes, particularly *Plagiothecium* (Figure 6) and *Rhodobryum roseum* (Figure 7), under heavy grazing pressure of sheep in an alpine habitat in southern Norway.



Figure 6. *Plagiothecium succulentum*, member of a moss genus that increases under heavy grazing of sheep in alpine areas of southern Norway. Photo by Hermann Schachner, through Creative Commons.





Figure 7. *Rhodobryum roseum*, a moss species that increases under heavy grazing of sheep in alpine areas of southern Norway. Photo by Hermann Schachner, through Creative Commons.

In a study of ruminants from the Canary Islands, Rodríguez Suárez *et al.* (1990) found that mouflons [wild sheep; *Ovis aries musimon* (Figure 8) – an endangered species that has been successfully cloned (Loi *et al.* 2001; Trivedi 2001)] and Barbary sheep (*Ammotragus lervia*; Figure 9), native of northern Africa and introduced to Europe in the late 1800's) consumed bryophytes. Rodríguez Suárez and coworkers examined the stomach contents of 46 Corsica mouflons and 19 Barbary sheep from the highest area of La Palma and Tenerife islands. They found that 11 stomachs contained *Grimmia laevigata* (Figure 10), *Grimmia* sp., *Racomitrium heterostichum* (Figure 11), and 2 *Didymodon* sp. (Figure 12). These species grow on rocks in very dry habitats where other plants usually considered more suitable for consumption are generally absent. This suggests that the consumption of mosses is deliberate.



Figure 8. Mouflon (*Ovis aries musimon*), a moss consumer. Photo through Creative Commons.



Figure 9. Barbary sheep (*Ammotragus lervia*), a moss consumer, eating. Photo by Peripitus, through Creative Commons.



Figure 10. *Grimmia laevigata*, a moss species consumed by mouflons and Barbary sheep in the Canary Islands. Photo by Hermann Schachner, through Creative Commons.



Figure 11. *Racomitrium heterostichum*, a moss species consumed by mouflons and Barbary sheep in the Canary Islands. Photo by J. C. Schou, with permission.





Figure 12. *Didymodon rigidulus* var. *icmadophilus*, in a moss genus sometimes consumed by mouflons and Barbary sheep in the Canary Islands. Photo by Michael Lüth, with permission.

Like the roe deer (*Capreolus capreolus*; Figure 13), grazing sheep are often transporters of bryophyte fragments and other propagules (Müller & Heinken 2011). Pauliuk *et al.* (2011) compared transport by two breeds of sheep. The twelve sheep in the study carried 16 species of mosses, but these represented only 40% of the moss species in the pasture (Figure 14). The belly and tail (Figure 13) were especially good at transport. The two breeds favored different species and frequencies. Those sheep that had a dense, curly fleece were able to carry larger species and more fragments than the breed with a fine, smooth fleece. The horizontally growing pleurocarpous mosses, as with roe deer, were more common than upright acrocarpous species; small species and mats were likewise more common than other forms. Large species, acrocarpous species, wefts, and turfs were underrepresented. Hooves, on the other hand, carried primarily acrocarpous colonist species.



Figure 13. Roe deer (*Capreolus capreolus*) lying down, a position that can put bryophyte fragments on the underbody and tail. Photo through Creative Commons.

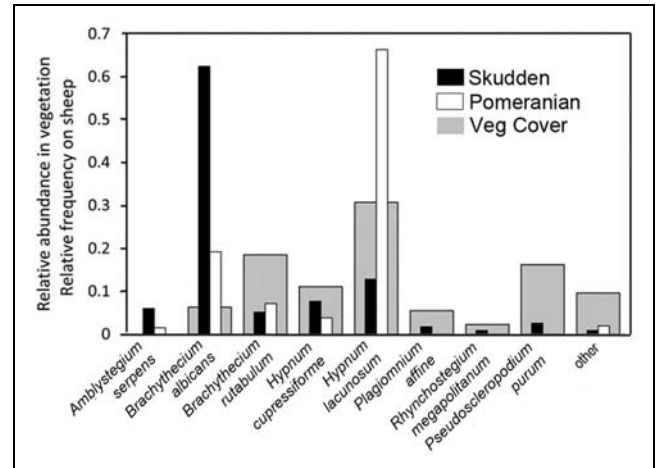


Figure 14. Comparison of bryophyte transport by two breeds of sheep: Skudden (n = 5, 117 fragments) and Pomeranians (n = 7, 2096 fragments). Grey bars indicate relative cover in the vegetation of the study site. Modified from Pauliuk *et al.* 2011.

It appears that at least some bryophytes receive other benefits from the sheep. They appear to maintain a habitat where these bryophytes can thrive. When the pasture is abandoned, bryophytes disappear due to their limited ability to compete with the invading tracheophytes (Takala *et al.* 2012). In southwestern Finland, cover, species richness, species density, and species diversity of bryophytes were all significantly higher in pastures that had been continuously grazed than those in abandoned grasslands. Takala defined three grassland habitats: (1) continuously grazed pastures, (2) previously abandoned pastures where grazing was re-established during 1990s, and (3) abandoned pastures. Among these, 17 species of bryophytes were suitable indicators of the three grassland types. Four of these indicated valuable grassland habitat.

In some areas, sheep graze in bogs (Rawes 1983). In two high altitude blanket bogs in the North Pennine uplands of England, cessation of sheep grazing led to major changes in the species composition, vegetation pattern, and structure of the bogs. Colonization of bare peat was slow in the exclosures. In particular, the leafy liverwort *Diplophyllum albicans* (Figure 15) declined, whereas it had previously been a constant companion for the cottongrass *Eriophorum* (Figure 16).



Figure 15. *Diplophyllum albicans*, a leafy liverwort species that declines in the absence of sheep. Photo by Hermann Schachner, through Creative Commons.





Figure 16. Cottongrass (*Eriophorum vaginatum*), member of a common genus in peatlands of English uplands. Photo through Creative Commons.

Lee *et al.* (2013) examined blanket bog plant communities following various types of disturbance, including low-intensity sheep grazing. In the low-intensity grazing areas, *Hypnum jutlandicum* (Figure 17) cover and bryophyte species richness both increased in the least-disturbed plots. Overall bryophyte cover, however, did not. In fact, low-level grazing had little impact on the bryophyte communities. The most-disturbed plots, with a 10-year burn cycle, had an increase in *Sphagnum* spp. (Figure 18) over a 10-year period. I have to wonder if drafts created by the burning contributed to dispersal from neighboring communities.



Figure 17. The moss *Hypnum jutlandicum* with capsules. Photo by J. C. Schou, through Creative Commons.



Figure 18. *Sphagnum girgensohnii*, representing a genus that increases in number of represented species following fire disturbance. Photo by Jutta Kapfer, with permission.

A common bryophyte in northern open areas is the moss *Racomitrium lanuginosum* (Figure 19). On a Scottish montane plateau, an area was fenced to provide a ski corridor (Scott *et al.* 2007). This area was used to establish permanent quadrats for a 12-year study. The fencing created a gradient in snow-lie and sheep use. *Racomitrium lanuginosum* cover was initially lower immediately adjacent to the fence. After 12 years, cover was reduced significantly in the 10 m adjoining the fence, whereas it was relatively stable further away. Scott and coworkers attributed the decline near the fence to greater snow-lie and heavier sheep usage. Grass cover near the fence increased. At the same time, *Dicranum fuscescens* (Figure 20) increased significantly near the fence. At more interior locations, there was a significant increase in *Polytrichastrum alpinum* (Figure 21) (Welch *et al.* 2005).



Figure 19. *Racomitrium lanuginosum* (white), a common moss species in Arctic and alpine areas, in Iceland. Photo by Manfred Morgner, through Creative Commons.



Figure 20. *Dicranum fuscescens*, a moss species that increased near the exclosure fence. Photo by Michael Lüth, with permission.

During and Willems (2003) reported that many species of mosses have disappeared "almost completely" from the Dutch chalk grasslands (see Figure 22) after grazing ceased. These included characteristic acrocarpous mosses such as *Tortella* spp. (Figure 23), *Trichostomum* spp. (Figure 24), *Aloina* spp. (Figure 25), and *Pleurochaete squarrosa* (Figure 26), but also the pleurocarpous species *Abietinella abietina* (Figure 27) and *Homalothecium lutescens* (Figure 28) have experienced drastic reductions. Litter indicator species such as *Brachythecium rutabulum*



(Figure 29) are concurrently increasing. As in other studies, these changes seem to be the result of cessation of grazing.



Figure 21. Alpine hairy cap moss, *Polytrichastrum alpinum*, with capsules, a species that increased in interior regions of exclosure fence. Photo by David T. Holyoak, with permission.



Figure 22. Chalk grassland similar to those in the Netherlands. Photo by Rose and Trev Clough, through Creative Commons.



Figure 23. *Tortella tortuosa*, a species that has disappeared from pastureland after grazing ceased. Photo by Hermann Schachner, through Creative Commons.



Figure 24. *Trichostomum crispulum*, in a moss genus that lived in Dutch chalk grasslands but has disappeared where grazing is no longer present. Photo by David T. Holyoak, with permission.

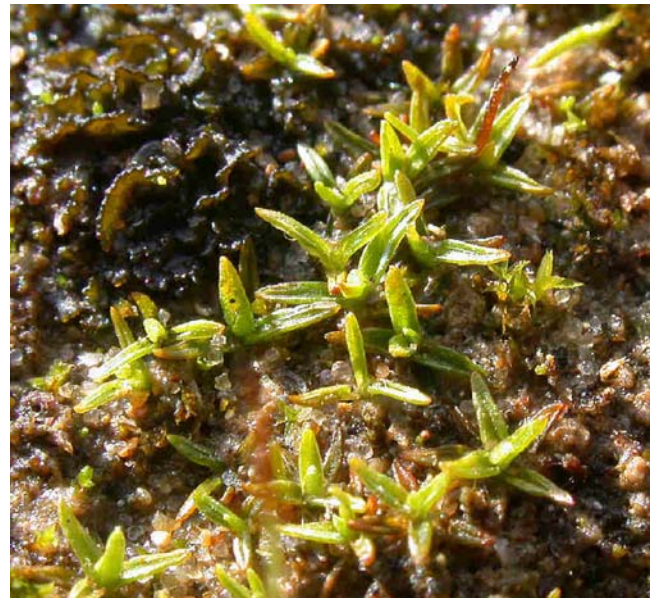


Figure 25. *Aloina aloides*, in a moss genus that lived in Dutch chalk grasslands but has disappeared where grazing is no longer present. Photo by David T. Holyoak, with permission.



Figure 26. *Pleurochaete squarrosa*, a moss species that lived in Dutch chalk grasslands but has disappeared where grazing is no longer present. Photo by David T. Holyoak, with permission.





Figure 27. *Abietinella abietina*, a species that has experienced severe decreases from pastureland after grazing ceased. Photo by Hermann Schachner, through Creative Commons.



Figure 28. *Homalothecium lutescens*, a species that has experienced severe decreases from pastureland after grazing ceased. Photo by J. C. Schou, Biopix, with permission.



Figure 29. *Brachythecium rutabulum* with capsules, a species that has increased in Dutch chalk grasslands after grazing was withdrawn. Photo by J. C. Schou, with permission.

Maelfait *et al.* (2007) similarly found that when dune vegetation was short-grazed by sheep (*Ovis aries*; Figure 30), the previously lichen-moss domination decreased. But one site changed during the same time to a cover of ~95% clipped grasses, mosses, and herbs, a physiognomy created by the grazing of sheep.



Figure 30. *Ovis aries*, domestic sheep that causes lichen-moss domination to decrease. Photo through Creative Commons.

One of the operators in the moss vs tracheophyte story in pastureland is nitrogen (van der Wal *et al.* 2003). Air pollution has increased nitrogen deposition, causing massive invasion of grasses, sedges, and rushes in habitats ranging from forests to upland heaths. At the same time, grazing by livestock has increased in many locations, further degrading natural ecosystems. In the Scottish montane ecosystem, grazing and nitrogen deposition interact, causing a loss of the moss-dominated habitat and takeover by grasses and sedges.

One of our techniques to maintain diversity is to create green spaces where normal (non-pasture) vegetation is allowed to grow. However, even in these situations adjacent land use can significantly alter the bryophyte (and tracheophyte) communities of the natural vegetation (Piessens *et al.* 2008). Fortunately, these effects occur only within 5 m or less of the borders into heathland patches. In these transition zones adjacent to the borders, the invasive moss *Campylopus introflexus* (Figure 31) is common at grazed sites.



Figure 31. *Campylopus introflexus*, an invasive moss species common in transition zones of grazed areas. Photo by Fitis-Sytske Dijkse, with online permission through <freenatureimages.com>.

Hill *et al.* (1992) found that *Polytrichum commune* (Figure 32) declined steadily in sheep exclosures (Figure 34) in Snowdonia, Wales. When sheep were fenced out of some areas, *Polytrichum commune* declined consistently,



presumably due to competition for light by larger tracheophytes. Subsequent to sheep exclosure (Figure 33-Figure 35), voles became dominant among the herbivores and considerable growths of pleurocarpous mosses like *Hylocomium splendens* (Figure 3) and *Pleurozium schreberi* (Figure 36) invaded the mats of dead grass.



Figure 32. *Polytrichum commune* with capsules, a species that declines when sheep are removed. Photo by Bas Kers, through Creative Commons.



Figure 33. Nature Reserve, Helfdi, Iceland, in area where sheep are allowed to browse. Photo by Janice Glime.



Figure 34. Nature Reserve, Helfdi, Iceland, in exclosure where sheep are unable to browse. Photo by Janice Glime.



Figure 35. Wool on fence and plants on near side of fence in Iceland where grasses have been eaten by sheep. The exclosure prevents browsing on the opposite side where the grass is abundant. Photo by Janice Glime.



Figure 36. *Pleurozium schreberi*, a species that becomes dominant among dead grass in sheep exclosures when voles invade. Photo by Rob Routledge, through Creative Commons.

But do sheep eat bryophytes? Rodríguez Suárez *et al.* (1990) reported 15 cryptogams in the stomachs of goats and sheep. The winter diet of feral Soay sheep (*Ovis aries*; Figure 30) at St. Kilda, Scotland, is comprised of 20-30% mosses (Milner & Gwynne 1974). When Virtanen and Crawley (2010) assessed the relationships of bryophytes with these St. Kilda sheep, they found that bryophytes and tracheophytes had opposite trends relative to elevation and sheep preference. The bryophytes reached their highest species richness at mid to high elevations and were negatively correlated with levels of sheep preference.

In a 1500 m<sup>2</sup> plot in a sheep pasture of the Netherlands, the moss layer disappeared almost totally, concomitant with the introduction of artificial fertilizer application and liquid manure (Arnolds 1989). This coincided with changes in the fungal populations, and those fungi associated with litter or bryophytes decreased in numbers.

In the alpine communities of the Scottish Highlands (Figure 37), one can find rare species (Miller *et al.* 2010). Nevertheless, this community is often heavily grazed by sheep. Many have suggested that the sheep hold the community in a **plagioclimax** (habitat or area in which influences of humans have prevented further ecosystem development). By excluding sheep from spring until fall for 10 years, Miller and coworkers found that graminoids initially increased in cover and the vegetation became taller. However, this stage did not last, and a decline in



graminoid cover followed, with bryophytes becoming much more abundant. Permanent removal of sheep could cause a shift to a bryophyte-rich habitat tall-herb or scrub vegetation.



Figure 37. Alpine area in Scotland, where sheep often graze. Photo through Flickr Creative Commons.

Large herbivores can have an especially severe effect on bryophytes and other plants in Arctic and alpine regions (Austrheim *et al.* 2007). Using exclosures in an oceanic alpine ecosystem to stop sheep grazing, Austrheim and coworkers found that tracheophyte height increased, but the grass *Deschampsia flexuosa* (Figure 38) was the only tracheophyte that increased in cover in these exclosures. At the same time, six bryophyte species changed in abundance, favoring successional bryophytes. The mosses *Straminergon stramineum* (Figure 39) and *Pohlia nutans* (Figure 40) and the leafy liverwort *Cephalozia bicuspidata* (Figure 41) increased when sheep grazing ceased.



Figure 38. *Deschampsia flexuosa*, the only seed plant in an oceanic alpine ecosystem that increased in cover inside sheep exclosures. Photo by M. Porto, through Creative Commons.



Figure 39. *Straminergon stramineum*, a species in an oceanic alpine ecosystem that increases when sheep grazing stops. Photo by Jutta Kapfer, with permission.



Figure 40. *Pohlia nutans* in Svalbard, a moss that benefits when sheep grazing stops. Photo by Michael Lüth, with permission.



Figure 41. *Cephalozia bicuspidata*, a leafy liverwort species that increases when sheep grazing stops. Photo by Botany Website, UBC, with permission.

For *Pohlia nutans* (Figure 40), this is a surprise as it tends to occur in open, disturbed sites, and it also typically disappears when reindeer are fenced out (see above). Species of the mosses *Brachythecium* (Figure 29) and *Plagiothecium* (Figure 6) likewise decreased in the exclosures, while *Polytrichum* (Figure 32) species actually



increased with grazing, as already noted in Wales by Hill *et al.* (1992) and elsewhere (Helle & Aspi 1983; Väre *et al.* 1996; Virtanen 2000; Olofsson *et al.* 2004), causing Austrheim *et al.* (2007) to consider the genus to be grazing resistant. The leafy liverworts *Barbilophozia lycopodioides* (Figure 42) and *B. floerkei* (Figure 43) decreased with grazing, whereas the latter disappeared in the exclosures in the Arctic reindeer study by Väre *et al.* (1995), where it was replaced by the lichen *Cladina* (Figure 44), a preferred food of reindeer. Nevertheless, exclosures did not result in changes in tracheophyte or bryophyte species richness or total cover of bryophytes and lichens in the Austrheim *et al.* study. A side effect of the exclosures and cessation of sheep grazing was that rodent grazing was also reduced.



Figure 42. *Barbilophozia lycopodioides*, a leafy liverwort species that diminishes with sheep grazing. Photo by Hermann Schachner, through Creative Commons.



Figure 43. *Barbilophozia floerkei*, a species that decreases with grazing but can disappear in exclosures. Photo by Hermann Schachner, through Creative Commons.



Figure 44. *Cladina* spp., a genus that replaces *Barbilophozia floerkei* in reindeer exclosures in the Arctic. Photo by Peder Curman, through Creative Commons.

## Goats – *Capra*

Goats are known to eat everything, right? So we shouldn't be surprised that in Washington State's Olympic National Park (Figure 45), invasive goats, introduced from Canada and Alaska for hunting, were destroying the sensitive ecosystem (Wright 1996). In particular, the very rare Olympic Mountain milk vetch (*Astragalus cottonii*; Figure 46) was a favorite food. But like we might expect of goats, these goats ate everything, including mosses. They further affected the habitat by trampling and wallowing. Rodriguez Suárez *et al.* (1990) also found that goats on the Canary Islands consumed mosses.



Figure 45. Olympic rainforest, Washington, USA, with bigleaf maples and epiphytic mosses. Photo from NPS, through public domain.



Figure 46. *Astragalus cottonii*, a rare but favorite food of goats in the Olympic Mountains, USA. Photo by Paul Slichter, with permission.

Nevertheless, feral goats (*Capra hircus*; Figure 47–Figure 48) in New Zealand avoided mosses, even though mosses were very abundant compared to preferred foods like *Schefflera digitata* (Figure 49) and ferns (Mitchell *et al.* 1987).



Figure 47. *Capra hircus aegagrus*, a feral goat and moss avoider in New Zealand. Photo by Murat Göktaş through Creative Commons.





Figure 48. Wild goat, *Capra hircus aegagrus*, a goat that avoids eating mosses. Photo by Quartl, through Creative Commons.



Figure 49. *Schefflera digitata* in New Zealand, a preferred food of feral goats. Photo by Kahuroa, through Creative Commons.

### Cattle – *Bos*

It is hard to imagine a big cow choosing to eat mosses, but Esteban *et al.* (2012) reported that in the Southern Patagonian *Nothofagus* forests (Figure 50), mosses, along with grasses, were the most grazed vegetation by cattle (*Bos taurus*; Figure 51). But contrasting with many rodent herbivores, the cattle consumed erect herbs and mosses in the summer, switching to shrubs in spring and winter. In fact, while sheep primarily grazed prostrate herbs, cattle grazed mosses, except in autumn.

With this kind of preference for mosses, it might be surprising that removing cattle herbivory can cause a decline in bryophytes. But further examination in southwestern Finland reveals that these weak moss competitors are actually disappearing as tracheophyte biomass increases (Takala *et al.* 2012). By contrast, in continuously grazed grasslands, bryophyte cover, species richness, species density, and species diversity were significantly higher than in abandoned grasslands. The importance of cattle grazing for maintaining the bryophyte species richness is further supported by Humphrey and

Patterson (2000) in a riparian pasture and an upland conifer forest of the UK. Furthermore, they found almost no evidence that trampling had any effect on the bryophytes.



Figure 50. *Nothofagus pumilio* forest in Patagonia, a forest type where mosses are grazed by cattle (*Bos taurus*). Photo by through public domain.



Figure 51. *Bos taurus*, Italian cattle, a species that consumes mosses and herbs in summer, but shrubs in spring and winter. Photo by Justine Peacock, through Creative Commons

Yet Ludvíková *et al.* (2014a, b) found that in their experimental comparisons in temperate *Agrostis capillaris* (Figure 52) grassland, it was the non-trampled plots that had the highest composition of bryophytes, with *Rhytidiadelphus squarrosus* (Figure 53) being the dominant species (95%). However, the non-trampled plots also had the lowest evenness index, indicating few dominant species and lots of uncommon species. Soil compaction played an important role in determining species composition (Ludvíková *et al.* 2014b).





Figure 52. *Agrostis capillaris*, a dominant grass where the moss *Rhytidiadelphus squarrosus* co-exists where trampling is limited. Photo by Kristian Peters, through Creative Commons.



Figure 53. *Rhytidiadelphus squarrosus*, the dominant bryophyte in non-trampled plots in temperate grassland. Photo by Michael Lüth, with permission.

Ingerpuu and Sarv (2015) studied 15 Estonian coastal meadows (Figure 54) to compare effects of two different grazing pressures. During a 10-year period, the intensive grazing area experienced an increase in bryophyte diversity, but tracheophyte diversity did not increase, nor did that of the diaspore bank. Litter cover suppressed tracheophyte diversity. Nevertheless, tracheophyte and bryophyte diversity were positively correlated. And species composition remained unaffected by grazing intensity.



Figure 54. Estonian coastal meadow. Photo by KalervoK, through Creative Commons.

The Austrian agricultural landscapes (Figure 55) are rich in bryophytes, with a total of 506 species, 135 of which are considered to be endangered (Zechmeister *et al.* 2002). The upland landscapes dominated by moderately intensive cattle farming have significantly more endangered species than do the lowland landscapes with primarily intensive farming styles. Similarly, in comparing 24 grazed and 24 abandoned sites, Oldén *et al.* (2016) demonstrated that grazing had more impact on tracheophytes than on bryophytes in boreal wooded pastures. These are low-intensity livestock grazing areas in forested sites.



Figure 55. Austrian agricultural landscape. Photo through Creative Commons.

In Finnish seminatural grasslands, Takala *et al.* (2014) used 420 plots in 21 grasslands to examine species richness and cover of bryophytes. They found that grazing promotes bryophyte species richness, with colonists and perennial bryophytes in particular increasing. As expected, colonists were strongly associated with sites having a high proportion of bare ground.

Among the most sensitive ecosystems that must endure grazing are the cryptogamic crusts (Figure 56) in prairie areas. In a study in southeastern British Columbia, Rosentreter (2006) found that rock cover decreased significantly(?),  $p > 0.10$ , in the Cattle Only Area from 1994 to 2004, whereas in the Wildlife Only Area there were no significant changes in litter, soil, bryophyte, or rock cover. Bryophytes and litter provided the predominant soil cover. But bryophyte cover overall increased nearly 70% from



1991 to 2003 ( $p < 0.10$ ), somewhat complicating the comparisons. Decreases in bryophyte cover in the exclosure area was driven by the increases in vascular plants and litter cover. Hence, bryophyte cover decreased with time in the exclosure, only the bryophytes increased in the wildlife and cattle area, and bryophytes did not change in the cattle only or wildlife only areas. Bryophytes are important contributors to these ecosystems by providing soil stability, nitrogen fixation, maintaining greater soil moisture, preventing runoff, facilitating infiltration, and enhancing seed germination and subsequent plant growth (Anderson *et al.* 1982a, b; Johnston 1997; McCune 2000).



Figure 56. Cryptogamic crust in Natural Bridges National Monument, Utah. Photo by Hihonjoe, through Creative Commons.

Some endangered species are benefitted by cattle and pony grazing. The disturbance by the cattle and wheel ruts in salt marshes (Figure 57) where they graze creates open soil patches that can be colonized by *Bryum marratii* (Figure 58) (Holyoak 2015). But the occurrence of the species in wheel tracks was short-lived because grazing was light and competitive grasses (*Agrostis stolonifera*; Figure 59) excluded it within two years (Callaghan 2017). In Ireland, when salt marsh grazing stopped, a dense saltmarsh grass cover developed, leading to extinction of the moss in Northern Ireland and threatening the species in other Irish locations (Lockhart *et al.* 2012).



Figure 57. *Bryum marratii* habitat at bay of Meallabhan, Scotland, a salt marsh. Photo by Michael Lüth, with permission.

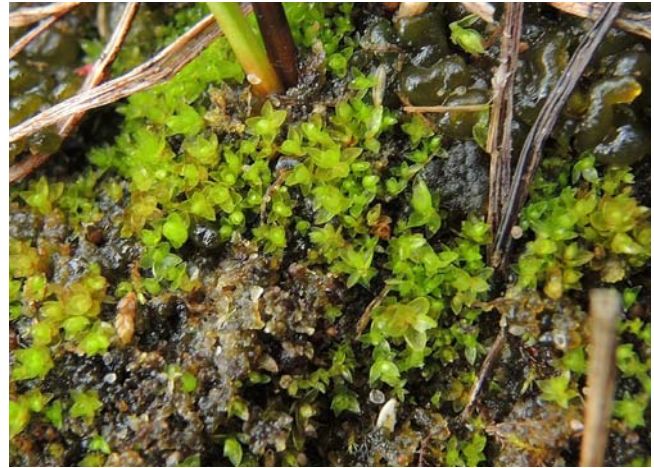


Figure 58. *Bryum marratii*, in a salt marsh in Scotland. Photo by Michael Lüth, with permission.



Figure 59. *Agrostis stolonifera*, a salt marsh species that crowds out *Bryum marratii*. Photo by Matt Lavin, through Creative Commons.

### Bison – Bison

Even large, herbivorous, late Pleistocene mammals such as the Mylakhchinsk bison (see Figure 60-Figure 61) have died with bryophytes in their alimentary tract (Ukrainitseva *et al.* 1978; Ukrainitseva 1979).

Ukrainitseva (1981) examined the gastrointestinal tracts of a variety of herbivorous mammals, including *Bison* (Figure 60-Figure 61), preserved from various periods during the Kargin interglacial period in the Indigirka River basin (Wisconsin period, 45,000-30,000 BP). During that time bogs spread, concurrent with the reduction of herbaceous communities suitable for pasturing. At the same time, rumen analysis indicated that the food composition changed for these large mammals, shifting to plants (Ukrainitseva *et al.* 1978), including *Sphagnum* (Figure 62), from moist and water-logged communities (Ukrainitseva 1981). These plants had considerably different nutrient quality, and the diet change led to the extinction of some of the herbivores.





Figure 60. American buffalo, *Bison bison*, grazing. The Mylakhchinsk bison died with mosses in its gut. Photo through Creative Commons.



Figure 61. The European bison, *Bison bonasus*, grazing amid grasses and mosses. Photo by Michael Gäbler, through Creative Commons.



Figure 62. *Sphagnum austinii*; species of *Sphagnum* entered the food chain when climate change caused more bogs to develop. Photo by Michael Lüth, with permission.

## Summary

Activities of sheep and other ruminants can contribute to dispersal of bryophytes as the fragments adhere to hooves and fur/hair/wool.

Many goats eat mosses, but feral goats in New Zealand seem to avoid them. Musk oxen may actually lose nutrients due to adsorption onto mosses they accidentally ingest. On the other hand, some sheep (*Ovis*) will eat bryophytes as a significant portion of their diet. Some goats (*Capra*) will eat them and others

avoid them. In southern Patagonia, cattle (*Bos taurus*) will eat mosses in summer, but not in winter.

When grazing is light, it can favor such mosses as *Rhytidiadelphus squarrosus*, *Polytrichaceae*, *Brachythecium*, and *Plagiothecium*. Colonizers like *Pohlia nutans* can benefit from disturbance and increased light. Leafy liverworts like *Barbilophozia lycopodioides* and *B. floerkei* decrease with grazing. Similarly, the moss *Straminergon stramineum* and the leafy liverwort *Cephalozia bicuspidata* benefit from exclosures. But the bryophyte communities depend on the site, with Arctic and alpine communities responding differently from more temperate ones. Rodents likewise can have a profound effect on the bryophytes, with communities responding differently depending on the foraging ruminants present.

Bryophytes suffer from manuring and urine, perhaps due to increased microbial decomposition, or to greater competition from the enriched tracheophytes.

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# CHAPTER 18-3

## LARGE MAMMALS – NON-RUMINANTS

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### TABLE OF CONTENTS

Canidae – Dogs .....	18-3-2
Macropodidae – Wallabies and Kangaroos .....	18-3-2
<i>Dendrolagus</i> – Tree Kangaroo .....	18-3-7
<i>Macropus</i> – Australian Wallabies (and others) .....	18-3-8
Vombatidae – Wombats .....	18-3-8
Phalangeridae .....	18-3-9
Common Brushtail Possum – <i>Trichosurus vulpecula</i> .....	18-3-9
Elephantidae – Elephants, Mammoths .....	18-3-10
Elephants – <i>Elaphas maximus</i> .....	18-3-10
Mammoths – <i>Mammuthus</i> .....	18-3-10
Ursidae – Bears .....	18-3-11
Hominidae – Primates .....	18-3-13
Chimpanzees .....	18-3-13
Summary .....	18-3-15
Acknowledgments .....	18-3-16
Literature Cited .....	18-3-16



# CHAPTER 18-3

## LARGE MAMMALS – NON-RUMINANTS



Figure 1. *Ursus americanus*, black bear cubs playing in mosses. Photo through public domain.

### Canidae – Dogs

When we think of the impacts of dogs (*Canis lupus familiaris*) on bryophytes, we tend to think of their habit of urinating (Figure 2) to mark their territory and record their presence. This raises concerns about permitting dogs on nature trails.

I was surprised to find a statement in 2012 that "very little is known about the nutrient composition of dog urine and its impacts on habitats" (White *et al.* 2012). Instead, these researchers refer to the ability of urine to "scald" vegetation, while acknowledging that it provides some enrichment of soil nitrogen (Taylor *et al.* 2005). White and coworkers also stated that dog urine does more damage on dry soils because the salts are unable to disperse quickly. Gilbert (1989) reported that dog urine has significant effects on algal crusts and lichen communities at tree bases. Unfortunately, bryophytes were not mentioned.

Webb (2002) studied the effects of human traffic, including dog walkers, in Lye Valley, Oxford, England. She found that the effect of dog urine was especially damaging to plants in very low nutrient ecosystems, like the calcareous fen areas and the dry calcareous grasslands.

The implication is that these negative effects included damage to fen mosses. Some fast-growing grasses benefit.



Figure 2. *Canis lupus familiaris* marking territory. Photo by Daniel Mott, through Creative Commons.



In urban areas, it is mostly *Bryum argenteum* (Figure 3) that finds its way into the cracks in the sidewalks and along their borders (Sam Bosanquet, Bryonet 8 June 2011). But in natural areas, rarer species may be affected. Bosanquet asked if anyone knew of the impacts of dog urine and feces on bryophytes, citing the known negative impacts of human urine on the leafy liverwort *Lepidozia cupressina* (Figure 4) and the filmy fern *Hymenophyllum tunbrigense* (Figure 5), often killing both.



Figure 3. *Bryum argenteum* in crack in parking lot. Photo by Paul Davison.



Figure 4. *Lepidozia cupressina*, a species that is negatively impacted by dog urine. Photo by Michael Lüth, with permission.



Figure 5. *Hymenophyllum tunbrigense*, a fern that is negatively impacted by urine. Photo through Creative Commons.

In her moss gardens, Annie Martin (Bryonet 9 June 2011) has observed frequent visits from a St. Bernard who left sizeable deposits of feces. Fortunately, this does not seem to have caused any harm to the garden, even if left there for several days.

Rod Seppelt (Bryonet 8 June 2011) relays his own experience. Mosses such as *Eurhynchium* (*Kindbergia*; Figure 6) and *Brachythecium albicans* (Figure 7) are able to regrow rapidly after urine damage, probably initially through lack of competition from the grasses that die off, but later come back. But dog urine is concentrated, so some bryophytes are likely to experience toxic effects. What seems to be the worst component for plants is ammonia, particularly the high concentration of nitrogen <www.dogster.com>. In the Arctic (Figure 8), urine enriches the nutrients, and if these nutrients are too high, seed plant vegetation benefits, to the detriment of the poorly competing bryophytes (see Chapter 18-1).



Figure 6. *Eurhynchium praelongum*, a species that regrows quickly after being sprayed with urine. Photo by Juan Larrain, with permission.



Figure 7. *Brachythecium albicans*, a species that regrows quickly after being sprayed with urine. Photo by Michael Lüth, with permission.





Figure 8. Tundra with dwarf willow, blueberry, and bearberry in Alaska, a habitat enriched by nutrients in urine of large mammals. Photo by Nathanael Coyne, through Creative Commons.

Bryophytes are known to require lower nutrient concentrations than that of tracheophytes. Cape and coworkers (2009) presented evidence that we should re-evaluate our perspective on the critical ammonia levels for plants. They suggested  $1 \mu\text{g NH}_3 \text{ m}^{-3}$  for bryophytes, whereas they suggested  $3 \pm 1 \mu\text{g NH}_3 \text{ m}^{-3}$  was appropriate for herbaceous tracheophytes.

As I read these comments about the lack of response of bryophytes to dog urine, I must wonder about the impact of climate on this seeming lack of response. In a humid climate where bryophytes remain hydrated and rain is frequent, might the urine be washed away before enough of it enters the moss to harm it? On the other hand, might a dry climate result in concentration and dose the moss with lots of it at once when rehydration occurs, especially with fog or night-time dew? Would the urine convert to uric acid and hence be more harmful in that state?

## Macropodidae – Wallabies and Kangaroos

Most wallabies don't seem to have a direct interaction with bryophytes, but they can have a major impact on them by damaging and browsing or grazing on competing vegetation. Unlike the damage done by deer and goats in other areas of New Zealand, the damage to vegetation on Kawau Island, New Zealand, is the result of four species of introduced Australian wallabies [*Macropus eugenii* – Dama wallaby (Figure 9), *Macropus parma* – parma wallaby (Figure 10), *Petrogale penicillata penicillata* – brush-tailed rock wallaby (Figure 11), and *Wallabia bicolor* – swamp wallaby (Figure 12)] (Wilcox *et al.* 2004). The activities of these wallabies in the forest damage the tracheophyte vegetation and create a lawn of bryophytes (Figure 13). This appears to be the result of greater tolerance on the part of bryophytes, rather than superior competition. The most common species are the mosses *Campylopus clavatus* (Figure 14), *Dicranoloma billardierei* (Figure 15), *Leucobryum candidum* (Figure 16), and *Ptychomnion aciculare* (Figure 17), especially *Dicranoloma billardierei*. A few patches of the large liverwort *Chandonanthus squarrosus* (Figure 18) are also present, with large areas of *Cladina* (Figure 19) and *Cladia* (Figure 20-Figure 21) lichens. The researchers consider

this lawn to be the result of superior tolerance of stress by the bryophytes and lichens.



Figure 9. *Macropus eugenii*, the Dama wallaby, with Joey. This species, introduced to New Zealand, destroys the ground vegetation, and it becomes replaced by bryophytes. Photo by Mathae, through Creative Commons.



Figure 10. *Macropus parma* (parma wallaby) with joey. This species, introduced to New Zealand, destroys the ground vegetation, and the vegetation is replaced by bryophytes. Photo by Matthias Kabel, through Creative Commons.





Figure 11. *Petrogale penicillata penicillata* (brush-tailed rock wallaby). This species, introduced to New Zealand, destroys the ground vegetation, and it becomes replaced by bryophytes. Photo by Roy at NatureMap, through Creative Commons.



Figure 14. *Campylopus clavatus*, a common species of moss in forest bryophyte lawns of Kawau Island following invasion of Australian wallabies. Photo from Canberra Nature, through Creative Commons.



Figure 12. *Wallabia bicolor* (swamp wallaby). This species, introduced to New Zealand, destroys the ground vegetation, which is replaced by bryophytes. Photo by Patrick K59, through Creative Commons.



Figure 15. *Dicranoloma billardiarei*, a common species of moss in forest bryophyte lawns of Kawau Island following invasion of Australian wallabies. Photo by Michael L  th, with permission.



Figure 13. Bryophyte lawn created by wallabies on Kawau Island, New Zealand. Photo courtesy of Mike Wilcox.



Figure 16. *Leucobryum candidum*, a common species of moss in forest bryophyte lawns of Kawau Island following invasion of Australian wallabies. Photo by Phil Bendle, through Creative Commons.





Figure 17. *Ptychomnion aciculare*, a common species of moss in forest bryophyte lawns of Kawau Island following invasion of Australian wallabies. Photo by Nathan Fell, through Creative Commons.



Figure 18. *Chandonanthus squarrosus*, a less common liverwort in forest bryophyte lawns of Kawau Island following invasion of Australian wallabies. Photo by David Tng, with permission.



Figure 19. *Cladina mitis*; the genus *Cladina* is common in forest lawns of Kawau Island following invasion of Australian wallabies. Photo by Triin Lillemets, through Creative Commons.



Figure 20. *Cladia retipora* lawn, in a common genus of lichen in forest lawns of Kawau Island following invasion of Australian wallabies. Photo by Chris Lindorff, through Creative Commons.



Figure 21. Close view of *Cladia retipora*, in a common genus of lichen in forest lawns of Kawau Island following invasion of Australian wallabies. Photo by Vanessa Ryan, through Creative Commons.

Sankaran *et al.* (2008) found that the eastern grey kangaroo (*Macropus giganteus*; Figure 22) and the common wombat (*Vombatus ursinus*; Figure 23), on the other hand, are more effective at increasing woody plant abundance than the introduced hog deer (*Axis porcinus*; Figure 24) or native swamp wallabies (*Wallabia bicolor*; Figure 12), both of which are browsers. The hog deer is the largest consumer of mosses (less than 0.01%) in southeastern Australia (Davis *et al.* 2008).

Hobbs (1996) likewise considered that browsing by herbivorous ungulates on grasses, forbs, and shrubs could give competitive advantage to trees, ferns, and mosses. This assumption is partly supported on Yanakie Isthmus (connecting Wilsons Promontory to mainland Victoria, Australia) by the observed increase in moss cover in their presence, while grass cover decreased (University of Ballarat 1999).





Figure 22. *Macropus giganteus*, eastern grey kangaroo, a species in New Zealand that is responsible for increasing woody plant abundance. Photo by Danielle Langlois, through Creative Commons.



Figure 23. *Vombatus ursinus*, common wombat, a species in New Zealand that is responsible for increasing woody plant abundance. Photo by P. Baum, through Creative Commons.



Figure 24. *Axis porcinus*, a browser that also eats mosses. Photo by Simon J. Tonge, through Creative Commons.

### *Dendrolagus* – Tree-kangaroo

The Lumholtz tree-kangaroo (*Dendrolagus lumholtzi*; Figure 25) is known from the rainforests of Northeast Queensland, Australia. It is the smallest (~0.5m body length) of the tree-kangaroos and is somewhat territorial. It consumes mosses, as well as lichens, ferns, and flowers (Heise-Pavlov 2017).



Figure 25. *Dendrolagus lumholtzi*, a moss consumer. Photo by Kenneth Bader, through Creative Commons.

Mosses seem to be more commonly consumed among the tree-kangaroos than among other wallabies. The Huon tree-kangaroo (*Dendrolagus matschiei*; Figure 26) is a generalist leaf eater, including leaves, fruits, and mosses in its diet (Betz 2001). In the rainforests of their native Papua New Guinea, they live where the forest floors are covered by a variety of moss species (Porolak 2008). Lichens and **lianas** (vines) are uncommon at the altitudinal range (1,000-3,000 m) where they live.

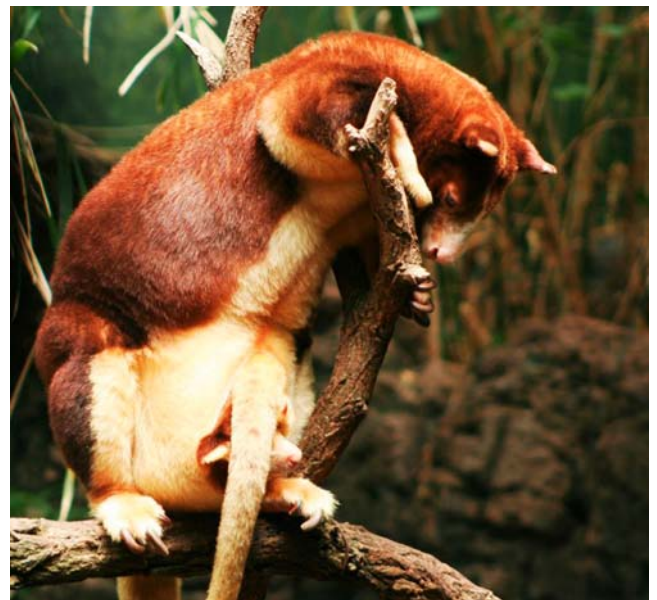


Figure 26. *Dendrolagus matschiei*, a generalist plant eater, including mosses. Photo by Cyndy Sims Parr, through Creative Commons.



### **Macropus – Australian Wallabies (and others)**

Species of *Macropus* (Figure 27) make **hip holes** to use as resting sites, especially in hot weather (Eldridge & Rath 2002). **Hip holes** are shallow, kidney-shaped depressions these kangaroos construct next to trunks of many trees and shrubs in arid and semi-arid Australia. Although these hip holes average less than 10 cm deep (Eldridge & Rath 2002), that is enough digging to cause considerable destruction to the thin cryptogamic crust of lichens, bryophytes, and bacteria (Eldridge & Greene 1994).



Figure 27. *Macropus parma*, a species introduced to New Zealand, that destroys the ground vegetation, which is replaced by bryophytes. Members of this genus destroy bryophyte vegetation by digging hip holes. Photo by Mistvan, through Creative Commons.

### **Vombatidae – Wombats**

Jones and Pharo (2009) questioned the importance of bryophytes in the buttongrass moorland in Australia following fire. Moss patches there become visible between the charred tussocks of grass. These researchers established twenty wire cages (30 cm x 30 cm x 20 cm) as exclosures that permitted insect access but not vertebrates. In addition, 20 patches with a minimum diameter of 10 cm of either of the mosses *Campylopus* spp. (Figure 14) or *Dicranoloma* spp. (Figure 15) were divided by a cage to test whether these mosses would become food to large herbivores after the fire. However, using stem length measurements, they were unable to find any differences in mosses inside and outside exclosures.

One possible reason for the absence of evidence is that suitable feeding grounds were close enough to the burned area that wombats did not need to rely on poor quality food sources such as mosses (Jones & Pharo 2009). For wombats, the mosses are hard to digest. They are hindgut fermenters (Hume 1999). Polyphenolic compounds in mosses can have antibiotic properties that inhibit the digestion of hindgut fermenters (Prins 1982). Interestingly, the Parks & Wildlife Service (2008) considered mosses to be a "particular delicacy" for the wombats, with native grasses being their primary food, as well as shrubs, roots,

sedges, bark, and herbs.. Triggs (1996) considered that some mosses provide the wombats with water when they are moist and green; they are ignored when they are dry.

Jones and Pharo (2009) also considered the possibility that the wombats might only consume the capsules, but no capsules were observed at the study site. However, in a different buttongrass moorland they had observed evidence of grazing on capsules of the moss *Tayloria tasmanica* (Figure 28). In another report, Lyn Cave (in Fife 2015) concluded that the primary habitat of *Tayloria tasmanica* is wombat dung. For some reason, little attention has been given to the potential of moss capsules as food.



Figure 28. *Tayloria tasmanica*, a dung moss species possibly grazed on by wombats. Photo by Niels Klazenga, with permission.

When large herbivores live at high elevations with deep snow cover, they face a challenge getting enough of the right foods to balance their needs. This is further complicated by the slow regrowth of alpine plant species following disturbance. Thus, Green *et al.* (2015) hypothesized that responses of wombats (*Vombatus ursinus*; Figure 23) to disturbance by fire at high elevations would differ from those at low elevations. To test their hypothesis, they examined the winter diet of common wombats in the Snowy Mountains of Australia in the ten years following a fire. Optimal foraging theory predicts that these herbivores should respond to scarce food resources by widening their food choices. However, these wombats expanded their diet choices only slightly at the higher elevations compared to those at the lower elevations, with no expansion in number of food species. Rather, they are able to exploit the improved food quality resulting from nutrients released by fire.

Wombats may actually contribute to bryophyte diversity. I have observed *Mittenia plumula* (Figure 29) growing at the entrance (Figure 30-Figure 31) of a wombat burrow. The opening provided the disturbed soil and cave environment needed by this species.





Figure 29. Close view of *Mittenia plumula*. Photo by David Tng, with permission.



Figure 30. *Mittenia plumula* in wombat burrow opening in Australia. Photo by Janice Glime.



Figure 31. *Mittenia plumula* in wombat burrow opening in Australia. Photo by Janice Glime.

## Phalangeridae

### Common Brushtail Possum – *Trichosurus vulpecula*

I doubt that the Australian possum uses bryophytes, but the moss uses it. I have seen the moss *Tayloria octoblepharum* (Figure 32) growing on the dung of the common brushtail possum (*Trichosurus vulpecula*; Figure 33) in Australia. Like other members of the *Splachnaceae*, this species uses dung as its substrate and the capsules smell like dung at maturity, attracting flies that disperse the spores.



Figure 32. *Tayloria octoblepharum* on possum dung at Rainbow Mountain, NZ. Photo by Janice Glime.



Figure 33. *Trichosurus vulpecula*; dung of this species is a substrate for the moss *Tayloria octoblepharum*. Photo by J. J. Harrison, through Creative Commons.



## Elephantidae – Elephants, Mammoths

### Elephants – *Elaphus*

One might expect elephants, the giants of the four-legged creatures, to be destructive of bryophytes, but in a *Sphagnum* (Figure 34) bog of Peninsula Malaysia, elephants (*Elephas maximus*; Figure 35) maintain the plant communities with their trampling (Yao *et al.* 2009).



Figure 34. *Sphagnum orientale*, a moss that can be found in bogs of the Malaysian Peninsula. Photo by Blanka Shaw, with permission.



Figure 35. *Elephas maximus* (Asian elephant). Ancestors of this genus perished in the Wisconsin era, perhaps due to the conversion of suitable pasture into bog habitat. Photo by Bernard Dupont, through Creative Commons.

### Mammoths – *Mammuthus*

The prehistoric woolly mammoth (*Mammuthus primigenius*; Figure 36) ate mosses – and became entombed in the ice with a meal of *Polytrichum* (Figure 37) and *Hypnum* (Figure 38) in its stomach (Bland 1971).



Figure 36. Woolly mammoth (*Mammuthus primigenius*), a prehistoric moss consumer. Image from Flying Puffin, through Creative Commons.



Figure 37. *Polytrichum commune*, possibly food of the woolly mammoth. Photo by J. R. Crellin, through Creative Commons.

On the other hand, van Geel *et al.* (2011) considered the mosses in the Palaeo gut sample from a mammoth calf from Yamal Peninsula, northwest Siberia, to be accidental. They considered that a one-month-old calf most likely ate fecal material that had been deposited on mosses and that associated mosses were consumed at the same time.





Figure 38. *Hypnum lindbergii*, possibly food of the woolly mammoth. Photo by Michael Lüth, with permission.

Ukrainseva (1981) similarly examined the gastrointestinal tract of large mammals from the Pleistocene, looking for possible causes of extinction. He found, using  $C^{14}$  analysis from the horse (*Equus*; Figure 39), mammoth (*Elaphas*; Figure 35), and bison (*Bison*; Figure 40), that these animals perished during the Wisconsin period, 45,000-30,000 BP. During that time period, bogs and forests spread while herbaceous communities (pastures) diminished, changing the quality of the food they consumed. Instead of their usual pasture food, they had to feed in water-logged sedge, cottongrass, grass, moss, and *Sphagnum* (Figure 34) communities. Hence their nutrient consumption changed, a change that Ukrainseva considered to be the cause of their extinction.



Figure 39. *Equus caballus* (Dartmoor pony). Ancestors of this genus perished in the Wisconsin period, perhaps due to the conversion of suitable pasture into bog habitat. Photo by Simon J. Tonge, through Creative Commons.



Figure 40. *Bison bison* (buffalo). Ancestors of this genus perished in the Wisconsin period, perhaps due to the conversion of suitable pasture into bog habitat. Photo through Creative Commons.

## Ursidae – Bears

Researchers have questioned whether bears consume bryophytes by choice. Elgmork and Kaasa (1992) contended that they are consumed only accidentally. But Dalen *et al.* (1996) reported that brown bear (*Ursus arctos*; Figure 41) feces contained 50-90% bryophytes, hardly an accidental percentage. Nevertheless, Dalen and coworkers found this only in May for a bear and her two cubs, again suggesting that bryophyte consumption was not a normal occurrence. At other times, some feces contained 15% *Brachythecium reflexum* (Figure 42), but it appeared that these mosses were consumed when the bears ate ants. Nevertheless, Wilson and Ruff (1999) noted that bears are omnivores, thus eating a variety of plant foods, including mosses.



Figure 41. *Ursus arctos arctos* (brown bear), a subspecies that eats lots of bryophytes. Photo by Jiří Bukovský, through Creative Commons.



Figure 42. *Brachythecium reflexum*, a species reaching as much as 15% of content in feces of the brown bear (*Ursus arctos*). Photo by Michael Lüth, with permission.

Iversen (2011; Iversen *et al.* 2013) studied the diet of polar bears (*Ursus maritimus*; Figure 43) from Svalbard. She reported 13 species of mosses in the feces, with *Polytrichastrum alpinum* (Figure 44) being the most frequent. Only 32.8% of the feces contained terrestrial vegetation. Of these, 27% contained mosses. Not only



were mosses relatively frequent, they also made up a significant portion of the biomass. Only two scats could be attributed to juveniles, but both contained mosses. On the other hand, Lønø (1970) found moss in only 2 of the 172 stomachs examined from Svalbard polar bears.



Figure 43. *Ursus maritimus* (polar bear), a moss consumer. Photo courtesy of Bob Krear.



Figure 44. *Polytrichum alpinum*, food of the polar bear on Svalbard. Photo by David Holyoak, with permission.

It appears that brown bears (*Ursus arctos*; Figure 41) have found another use for *Sphagnum* (Figure 48). The bears sometimes put peat mosses with carcasses that they cache, a behavior suggesting that the moss may be used to reduce bacterial and fungal attack on their food (Elgmork 1982). Hyvönen (1990) reported that bears often bury their prey in forests with mats of *Polytrichum* (Figure 37). Hyvönen reported on the Finnish coin that has a bear on one side and *Polytrichum* on the other side, suggesting that the association of these two organisms on the same coin related to the habit of the bears to bury their food in forests with *Polytrichum* ground cover.

Hyvönen (1990) reminds us that Linnaeus reported that bears (*Ursus arctos arctos*; Figure 41) gather *Polytrichum* (Figure 37) tufts to cushion their winter holes, whereas Dr. Erik Nyholm contends that bears are indiscriminate in choosing padding, using the more abundant species of *Pleurozium schreberi* (Figure 45) and *Hylocomium splendens* (Figure 46). They also seem to

use bryophytes for napping, as I have seen in several photographs posted on the internet.



Figure 45. *Pleurozium schreberi*, a species used by brown bears (*Ursus arctos arctos*) to pad their winter holes. Photo by Rob Routledge, through Creative Commons.



Figure 46. *Hylocomium splendens* on spruce forest floor, a species used by brown bears (*Ursus arctos arctos*) to pad their winter holes. Photo by Janice Glime.

Grizzly bears (*Ursus arctos* ssp; Figure 47) are a subspecies of brown bears, but are carnivorous (Wilson & Ruff 1999). Nevertheless, they reputedly eat moss, especially when they come out of hibernation, a report I have been unable to verify. Storie (1973) and Compton (1993) reported that grizzly bears eat unidentified mosses (Figure 48). It seems these bears eat mosses along with ants and soil when they are desperate, which doesn't say much for a discriminating appetite at that time!

Bears could damage some of the epiphytic bryophytes. They at times rip bark off trees to find insects for food (Zyśk-Gorczyńska *et al.* 2015). If bryophytes are growing there, they will come off with the bark. This leads me to wonder if the bears ever attempt to get insects from the mats of bryophytes on trees, another potential source of bryophyte destruction.

Bears are also known to contribute to the nutrient regime of bryophytes, but not as you might expect. They catch fish, then transport them to land (Figure 49) before consuming them. The remainder of the carcass provides a nitrogen source (Wilkinson *et al.* 2005).





Figure 47. *Ursus arctos* ssp. (grizzly bear), a species that consumes mosses in an effort to get the ants. Photo by Gregory Smith, through Creative Commons.

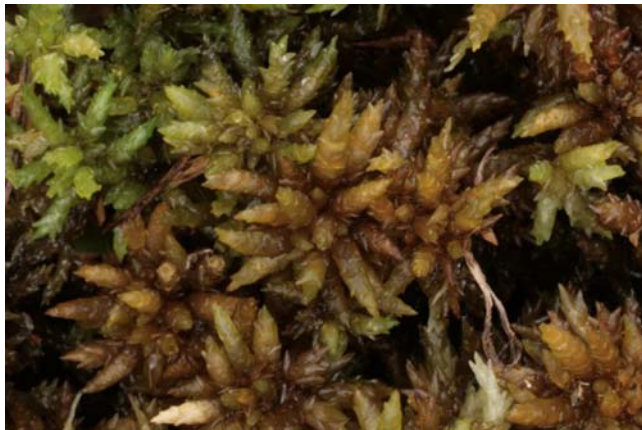


Figure 48. *Spaghnum perichaetiale*, a potential food source for grizzly bears in the Arctic. Photo by Jan-Peter Frahm, with permission.



Figure 49. *Ursus americanus* (black bear) carrying fish to land. Photo by Aaron Huelsman, through Creative Commons.

## Hominidae – Primates

### Chimpanzees

Eggar (1997) examined the habitats of China's monkeys, past and present. The environmental changes in the last 50 million years forced the animals to adapt to changing food availability. Some remained in the "diminishing rainforests" where they could find enough fruits and protein to survive. But others adapted to new

habitats. Among these adapters was the Yunnan snub-nosed monkey (*Rhinopithecus bieti*; Figure 50-Figure 51) that moved to the high-altitude pine forests (Figure 50). Here the most consistent food sources were hanging mosses and lichens on rocks.

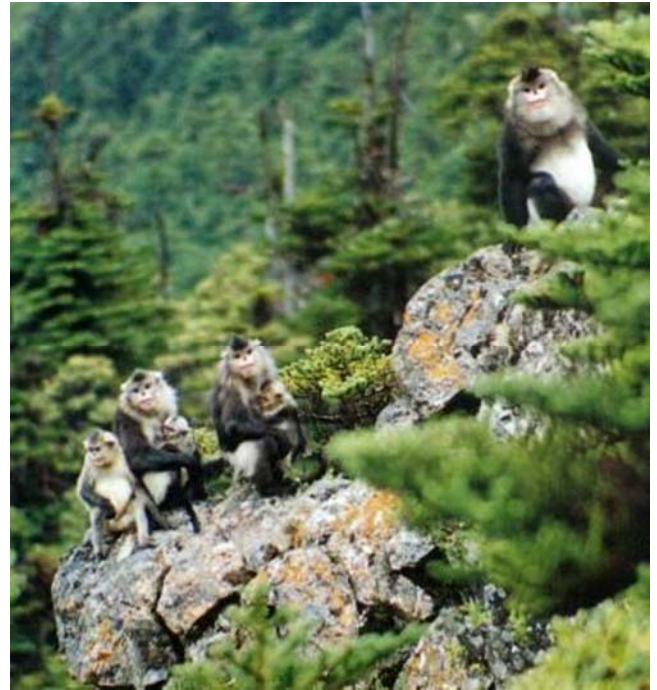


Figure 50. Yunnan snub-nosed monkey (*Rhinopithecus bieti*), a species that eats hanging mosses and lichens when it is forced to move to the mountains. Photo from EOL China Regional Center, through Creative Commons.

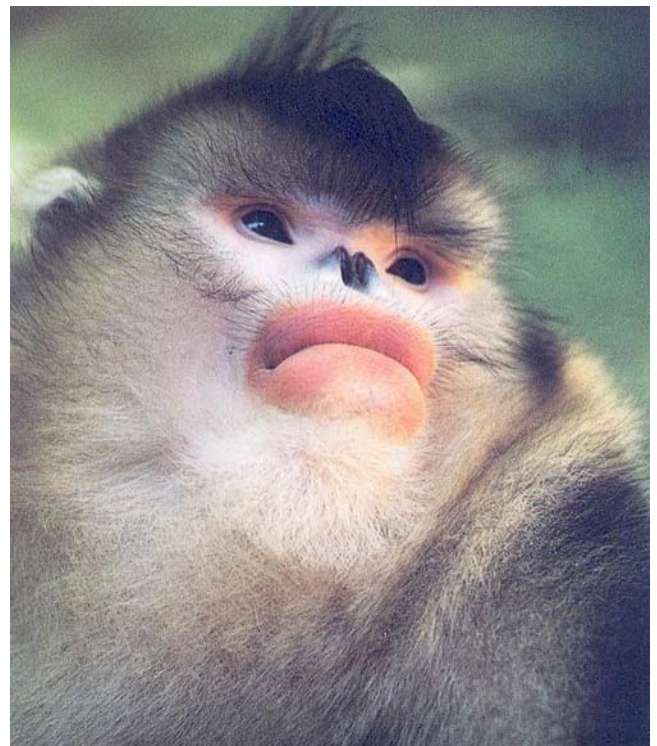


Figure 51. Close view of the Yunnan snub-nosed monkey (*Rhinopithecus bieti*). Photo from EOL China Regional Center, through Creative Commons.



But monkeys are smarter than most other animals. Lamon *et al.* (2017) were studying the behavior of wild chimpanzees (*Pan troglodytes*; Figure 52) in Budongo Forest Reserve in Western Uganda and discovered an unusual tool use. They were using mosses as sponges! This was a new behavior that first appeared in the population in 2011. Three years later, they found that the sponging behavior was still present and had spread to some of the other members of the community. Hanging mosses are common in areas inhabited by chimpanzees (Figure 53-Figure 56). The moss species used were *Pilotrichella cuspidata* (Figure 54), *Racopilum africanum*, and *Pinnatella minuta*, as well as two leafy liverworts – *Plagiochila strictifolia* and *Plagiochila pinniflora* (Hobaiter 2014).



Figure 52. *Pan troglodytes schweinfurthii* in its natural habitat. Photo by Bernard Dupont, through Creative Commons.



Figure 53. Hanging moss from Riparian forest, home of chimpanzees, Chappal Hendu, border of Cameroon, Taraba State Nigeria at 2000 m asl. Photo courtesy of Bup-Olu Oyesiku.

Three years after the initial 2011 moss sponging behavior, Lamon and coworkers (2017) decided to experiment to see if the mosses were a preferred method to obtain water. Using the same population that had learned the behavior, they selected a site where a clay pit had two ground water holes at the bottom of two trees. These cavities contained rainwater enriched with minerals. The experimenters hung the moss *Pilotrichella welwitschii* (see Figure 54), collected in swamp areas within the natural range of the chimpanzees, in trees around the clay pit. A wide choice of leaves was available naturally. Of 40

chimpanzees included in the study, 33 used moss sponges during at least one of the experimental trials. Five of these were among the original 8 sponge users and 17 were new at this behavior. Those who had tried the mosses seemed to prefer that method, as 18 of those 22 used only moss sponges to obtain water. Furthermore, Hobaiter *et al.* (2014) had noted only 8 of 32 individuals using moss sponges; leaf sponging was the predominant technique, with 83% of the individuals using it at least once and 18 were exclusive leaf spongers, although 22 chimpanzees used the mosses at least once. Three years later, mosses seemed to be the preferred tool among those that had learned the behavior.



Figure 54. *Pilotrichella* sp., one of the mosses used by chimpanzees for moss sponges. Photo by Lena Struwe, through Creative Commons.

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used the mosses at least once. Three years later, mosses seemed to be the preferred tool among those that had learned the behavior.

A similar sponging behavior occurred in chimpanzees (*Pan troglodytes*; Figure 55) in the Virunga National Park in the Democratic Republic of the Congo (Lanjouw 2002). When water was scarce, the chimpanzees gathered water from that collected in tree branches. When they could not access it directly, they prepared tools, including the use of sponges developed from mosses. The chimps collected mosses from trees. They then rolled them into a bundle about the size of a golf ball. These balls were inserted into the hollow of the branches. When the chimpanzees extracted the moss sponge, it had absorbed water. The chimpanzees sucked the water from the moss sponge, repeating this procedure to get additional drinks.



Figure 55. *Pan troglodytes* (chimpanzee) with moss sponge. Photo courtesy of Catherine Hobaiter.

The chimpanzees are known for getting water from the many hanging mosses in the rainforests (Min Chuah-Petiot, pers. comm. 1 March 2018). Among these hanging water sources are *Pilotrichella cuspidata*, *Squamidium brasiliense*, and *Papillaria africana* (Figure 56).



Figure 56. *Pilotrichella cuspidata*, *Papillaria africana*, and *Squamidium brasiliense* in Grande Comore, Africa, showing the hanging mosses that are typical of chimpanzee habitats where they are used as sponges. Photo courtesy of Min Chuah-Petiot.

## Summary

Large vertebrates may use bryophytes or harm them – or both. Dogs can damage them with urine and feces, but we have little scientific knowledge of these effects. Wallabies and kangaroos can damage the leafy vegetation, making the habitat suitable for bryophytes. *Dendrolagus* species, the tree-kangaroos, eat mosses. On the other hand, *Macropus* species, Australian wallabies, make hip holes, damaging the bryophytes as they dig.

Wombats make burrows, and mosses like *Mittenia* are able to establish on the recently disturbed soil at the opening. Some researchers suggest that wombats might consume mosses for their adhering water. They also consume capsules of the dung moss *Tayloria tasmanica*.

The dung moss *Tayloria octoblepharum* grows on the dung of the common brushtail possum (*Trichosurus vulpecula*).

Elephants can actually maintain some bryophyte communities through their trampling. And Pleistocene mammoths were preserved in ice with bryophytes in their gut. But a change from pasture habitats to boggy and mossy habitats may have led to their extinction.

Bears use the bryophytes to line the winter "nest." Others use growing bryophytes for napping. Bryophytes also occur in feces, but may be there through consumption of inhabiting ants. However, polar bears can eat large quantities of bryophytes. Brown bears also bury mosses with their food, presumably to help preserve the food. Bears can also drag fish into the forest to eat them, with the remains providing nutrients that benefit bryophytes.

The Yunnan snub-nosed monkey (*Rhinopithecus bieti*) subsists in a habitat where hanging mosses and rock lichens are the primary food source. Some chimpanzees (*Pan troglodytes*) in African rainforests have learned to use the pendent mosses as sponges to



gather water from tree holes and other difficult to reach places.

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Ron Porley kindly notified me of the publication on chimpanzees using mosses as sponges to drink. Jessica Beever provided me with the paper and helped me obtain the image of the moss lawn on Kawau Island, kindly provided by Mike Wilcox. Eileen Dumire critically reviewed the chapter.

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